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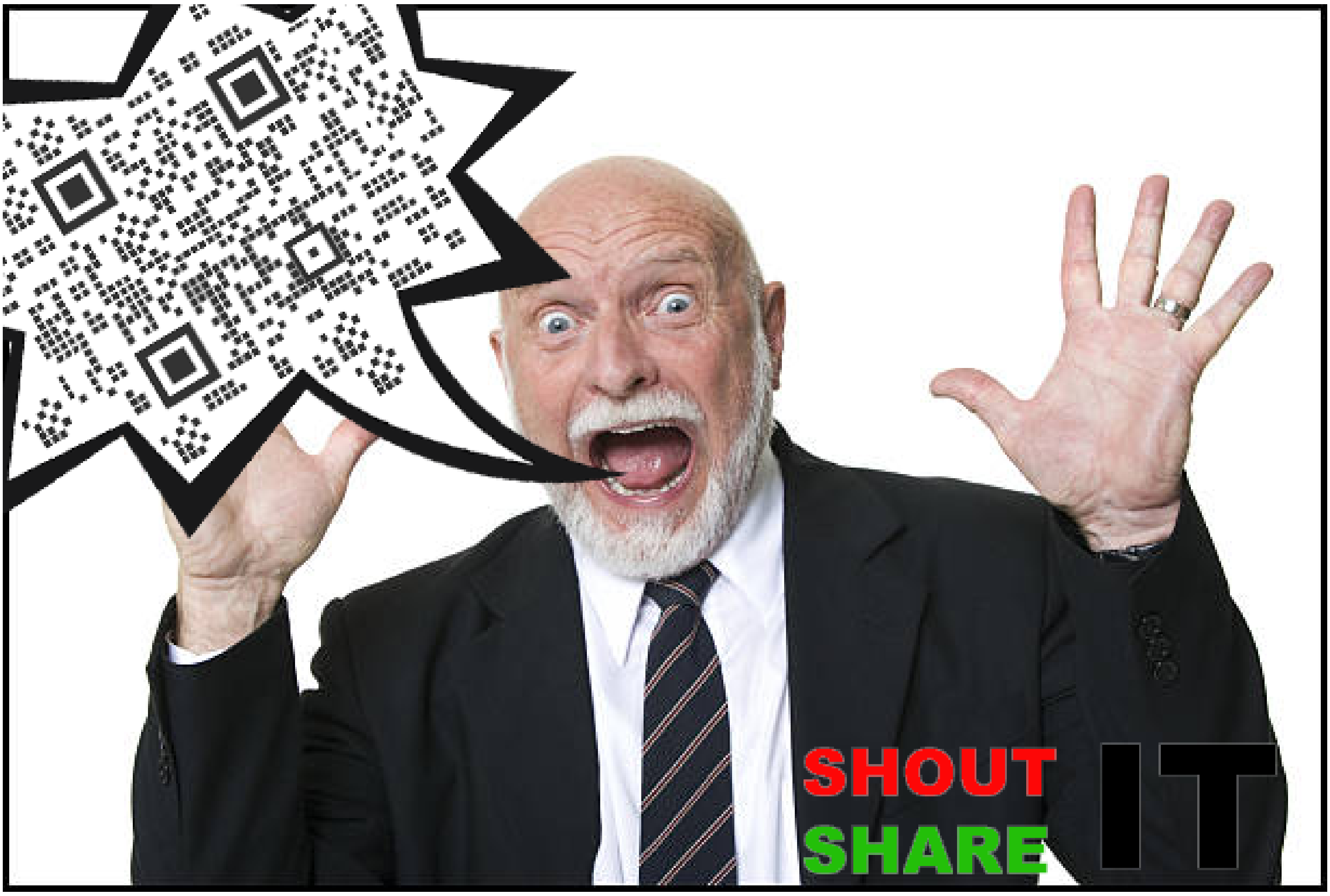
Studies in *Pseudocyphellaria* (lichens) I. The New Zealand species

David J. Galloway

Botany series Vol 17 25 February 1988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England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Bot.)

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The Botany series is edited in the Museum's Department of Botany
Keeper of Botany: Mr J. F. M. Cannon
Editor of Bulletin: Mr J. R. Laundon
Assistant Editor: Dr A. J. Harrington
Editor's Assistant: Miss M. J. Short

25 FEB 1988

ISBN 0 565 08018 0
ISSN 0068–2292

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Botany series
Vol **17** complete

Issued 25 February 1988

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(NATURAL HISTORY)
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Studies in *Pseudocyphellaria* (lichens) I. The New Zealand species

David J. Galloway

Department of Botany, British Museum (Natural History), Cromwell Road,
London SW7 5BD

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Synopsis

Forty-eight species of *Pseudocyphellaria* Vainio are recorded and described from New Zealand, and their known distributions there are mapped. Details of the chemistry, ecology, ecophysiology, and biogeography of *Pseudocyphellaria* are presented, together with a key to species; the generic concept and infrageneric classification are briefly discussed. *Pseudocyphellaria corbettii*, *P. haywardiorum*, *P. jamesii*, *P. lindsayi*, *P. nermula*, and *P. wilkinsii* are newly described, and the new combination, *P. pickeringii* (Tuck.) D. Galloway, is proposed.

Introduction

Species of *Pseudocyphellaria** are, in the main, conspicuous, leafy, foliose lichens best developed and with richest species diversity in rain-forest, shrubland, and successional vegetation, or subalpine and alpine grassland habitats of the Southern Hemisphere cool-temperate zone;

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* In many early accounts of New Zealand lichens, species of *Pseudocyphellaria* were referred to *Lobaria*, *Ricasolia*, *Sticta*, or *Stictina*. The genus name *Pseudocyphellaria* Vainio requires conservation, and a proposal to this effect is in preparation.

only a few taxa extend into tropical and/or Northern Hemisphere temperate, oceanic habitats. At present *c.* 110 species are known worldwide.

New Zealand is one of the two principal areas of endemism and speciation in the genus, the other being southern South America. Because of their often large size, ease of collection, and attractive colouring, species of *Pseudocyphellaria* were among the first lichens collected from New Zealand by early botanical explorers. William Lauder Lindsay (1829–1880) the Scottish doctor and lichenologist who botanized in the Otago settlement for several months in 1861 commented 'New Zealand is *par excellence*, the country of the *Stictae*. Not only do they there occur in the greatest absolute as well as relative numbers, but they there attain their maximum development, size and beauty . . . This preponderance of the *Stictae*, their frequently great size and beauty of colouring, and the profusion of individuals give a sometimes peculiar character to the foliaceous Lichen-flora of New Zealand' (Lindsay, 1869).

The luxuriance of growth and the species diversity of *Pseudocyphellaria* in New Zealand, together with its novel and complex array of secondary metabolites (see below under Chemistry) make it a genus of exceptional interest and significance. However, before species of *Pseudocyphellaria* can be used in a variety of important, applied studies, an accurate recognition of the taxa present in New Zealand is necessary, together with a stable system of nomenclature. In the 10 years that have elapsed since I and various collaborators first started work on *Pseudocyphellaria*, emphasis has, of necessity, been placed on the evaluation and solution of the often complex nomenclatural and taxonomic problems that the New Zealand and Southern Hemisphere species presented (Galloway, 1983*b*, 1985*a*, 1985*b*, 1986*a*, 1986*b*; Galloway & James, 1977, 1980, 1986; Galloway *et al.*, 1983*b*; Hawksworth & Galloway, 1984; Renner & Galloway, 1982). Recently, an introductory account of the New Zealand species appeared (Galloway, 1985*b*) dealing with 42 species.

In anticipation of future advances in cool-temperate lichen biogeography, chemistry, ecophysiology, and phytosociology, the present study of 48 species is offered as an introduction to an important group of Southern Hemisphere lichens.

Previous collections and research

The 18th century

The New Zealand botanical record begins with the *Endeavour* voyage of Captain Cook (1768–1771) and the collections of Joseph Banks and Daniel Carlsson Solander from various coastal localities, between 8 October 1769 and 31 March 1770. Godley (1983) states 'During these 174 days *Endeavour* was at anchor for 55 days and on 44 days the botanists went ashore. Their collection of some 360 species [this does not include lichens] was the first ever made of New Zealand plants. That it was such a comprehensive collection of the coastal and lowland plants of northern New Zealand resulted from a happy chance of a visit during the spring and summer'. From Cook's circumnavigation several coastal lichens were also collected, among the earliest from the Southern Hemisphere (Galloway, 1985*c*) and these collections, now in the herbarium of the British Museum (Natural History), contain four species of *Pseudocyphellaria* viz., *P. carpoloma*, *P. coronata*, *P. crocata* [annotated in pencil in Banks's hand 'Lichen 4 nova'], and *P. dissimilis* [annotated 'Lichen 5 nova'].

Cook's second voyage of 1772–1775 (David, 1981), subjected two main New Zealand localities to greater botanical scrutiny viz., Queen Charlotte Sound in Cook Strait and Dusky Sound in Fiordland, the latter named but not visited by Cook on the *Endeavour* voyage. Cook had with him on his second great circumnavigation the biologists J. R. and J. G. A. Forster and Anders Sparrmann (Du Rietz, 1981; Hoare, 1981, 1982; Lysaght, 1981) and from their collections the first published description of a Southern Hemisphere species of *Pseudocyphellaria* [as *Lichen berberinus* G. Forster] was made from material gathered in Tierra del Fuego (Forster, 1789; Galloway & James, 1977). The Forsters also collected in Dusky Sound, though in George Forster's *Florulae Insularum Australium Prodromus* (1786) the five lichens listed from Australia and New Zealand are only given Roman numerals and remain unnamed.

From Forster's New Zealand lichen collections [preserved in BM, LINN-SM, S, and UPS-THUNBERG- it is also possible that additional material may be found in Göttingen and Paris] Swartz (1781) named *Lichen filix* (*Sticta filix* (Sw.) Nyl.), the first Southern Hemisphere lichen to be described and illustrated and which was later depicted in colour engravings in both Hoffmann (1801) and Delise (1825*a*). Among Forster's known lichens (Galloway, 1981*c*), a specimen of *P. billardierei* is preserved in BM though no specific locality is given for it. William Anderson and Thomas Andrews also collected lichens at Dusky Sound (Galloway, 1981*c*) and in BM there is a specimen of *P. coronata* which is annotated 'Dusky Bay, Capt. Cook 1775'. The date here is in error, since Cook was in Dusky Sound from March to May, 1773.

The Scottish botanist Archibald Menzies (1754–1842), naturalist and later surgeon on Vancouver's *Discovery* voyage of 1791–1795 (Lamb, 1984; Galloway & Groves, 1987) was in Dusky Sound in 1791, and during his time there made the most extensive 18th century collection of New Zealand cryptogams. Among these were 16 lichen species in seven genera (Galloway, unpublished), with six being species of *Pseudocyphellaria* (*P. billardierei*, *P. cinnamomea*, *P. coronata*, *P. faveolata*, *P. lividofusca*, and *P. multifida*). A specimen of *P. aurata* (E) labelled by Menzies in pencil, probably when he was an old man as the handwriting is unsteady [the other collections are annotated by Menzies in ink], is most likely from a non-New Zealand tropical collection, as *P. aurata* does not occur anywhere in Dusky Sound.

The 19th century

For the first half of the 19th century published records of New Zealand material referable to *Pseudocyphellaria* (published initially under *Lobaria*, *Ricasolia*, *Sticta*, or *Stictina*) derive mainly from visits of either British or French botanists to North Auckland and/or to the subantarctic islands. The French were first on the scene and lichenological discoveries then made (including species of *Pseudocyphellaria*) were closely linked with the name of Dumont-D'Urville (Galloway, 1985*c*). On 11 August 1822 the corvette *Coquille*, under the command of Louis Isidore Duperrey, left Toulon on a round-the-world voyage to study terrestrial magnetism, meteorology, and natural history. Duperrey's second-in-command was J. S. C. Dumont-D'Urville, a botanist of some eminence, who was assisted by R. P. Lesson, elder brother of P. A. Lesson (botanist with D'Urville on the *Astrolabe*: 1826–1829). D'Urville and Lesson collected lichens from the Bay of Islands, northern New Zealand between 3–17 April 1824 (Galloway & James, 1986) and their collections are preserved in Paris (PC-LENORMAND and PC-THURET). Specimens of *Pseudocyphellaria* from the *Coquille* voyage were examined by Delise shortly after the expedition's return to France and from New Zealand material he described *Sticta carpoloma* Delise, and recorded *S. aurata* and *S. angustata* (Delise, 1825*a*, 1825*b*). The lichenological account of the *Coquille* voyage was prepared by Bory de St-Vincent (1829) who recorded *Sticta aurata* and *S. carpoloma* from Lesson's Bay of Islands collections.

D'Urville's second expedition (1826–1829) in the *Astrolabe* (the renamed *Coquille*) produced many important botanical discoveries in New Zealand, from the Thames estuary, and from Astrolabe Harbour on the Nelson shores of Cook Strait. Achille Richard's account of the New Zealand lichens discussed 27 taxa, among them four species of *Pseudocyphellaria* viz., *Sticta aurata*, *S. mougeotiana* [= *P. crocata*], *S. carpoloma*, and a new species, *S. cinnamomea* A. Rich, (Richard, 1832). The atlas of plates (Richard, 1833) contained handsome coloured engravings of *Sticta cinnamomea* and *S. carpoloma*. However, *Sticta carpoloma* sensu Richard is an entity with white pseudocyphellae (and not yellow as in *S. carpoloma* Delise), and is referable to *P. rufovirescens*. Montagne (1835) recognized Richard's description and illustration of *S. carpoloma* as a new species differing from *S. carpoloma* sens. str. when he noted 'S. carpoloma Rich. . . . non Delise, quae toto habitu cyphellisque citrinis distinctissima'. This new species he named *Sticta richardi* Mont., basing his description on material collected by Bertero from Juan Fernandez. Later, Montagne (1845, 1856) referred all similar New Zealand material (including the type of *P. rufovirescens*) to *S. richardi*; however, Juan Fernandez material is an independent taxon separable morphologically and chemically from the New Zealand *P. rufovirescens*.

Cunningham's (1836) account of the botany of northern New Zealand contains four species referable to *Pseudocyphellaria*, viz.; *S. aurata*, *S. carpoloma*, *S. cinnamomea*, and *S. mougeotiana*, based on the reports of Delise (1825*a*) and Richard (1832).

D'Urville's third Pacific expedition (1837–1840) visited the Auckland Islands and towards the end of the voyage several anchorages were made in New Zealand, first in Hooper's Inlet, Otago Peninsula, then in the wooded harbour of Akaroa (now ± completely deforested) where rich gatherings of *Pseudocyphellaria* were made, and finally, in the Bay of Islands. Collecting was under the charge of Jaques Hombron, senior surgeon of the *Astrolabe*, and Honoré Jacquinot, junior surgeon of the Zelée, with the senior surgeon of that vessel, E. Le Guillou, also collecting lichens. Their lichens from this time are preserved in Paris, the Akaroa collections of *P. rufovirescens* (including the type in BM) being particularly handsome and complete with elegant printed labels giving details of habitat, locality, date, and collector. The lichens of the voyage were published by Montagne (1845) who recorded *Sticta delisea* [= *P. glabra*], *S. faveolata*, *S. orygmaea* [= *P. coronata*], and *S. richardi* [= *P. rufovirescens*] from the Auckland Islands and Akaroa. The Atlas contains a sumptuous plate devoted to lichens with a fine coloured engraving of *P. coronata* (pl. 15, fig. 1).

However, it was the visit of J. D. Hooker to the Bay of Islands in 1841, during the Antarctic voyage (1839–1843) of the ships *Erebus* and *Terror* commanded by Capt. James Clark Ross, which gave lichenology in 19th century New Zealand its initial strong boost. Hooker, assistant-surgeon of H.M.S. *Erebus*, stayed three months at the Bay of Islands, and in company with David Lyall (assistant-surgeon of the *Terror*), William Colenso, and Andrew Sinclair, collected many lichens from northern coastal forests, as well as making good collections from the Auckland Islands and from Campbell Island. Hooker's Antarctic lichens which included those from New Zealand and Tasmania were prepared for publication by Thomas Taylor (Hooker & Taylor, 1844; Taylor & Hooker, 1845) and included 11 taxa referable to *Pseudocyphellaria* of which *Sticta glabra* J. D. Hook. & Taylor, *S. cellulifera* J. D. Hook. & Taylor [= *P. faveolata*], *S. linearis* J. D. Hook. & Taylor [= *P. billardierei*], *S. impressa* J. D. Hook. & Taylor [= *P. faveolata*], *S. flavicans* J. D. Hook. & Taylor, *S. coriacea* J. D. Hook. & Taylor, and *S. chloroleuca* J. D. Hook. & Taylor, were new taxa.

Raoul's (1846) list of 11 names referable to *Pseudocyphellaria* was taken from the accounts of Hooker & Taylor (1844) and Richard (1832), and added no new information.

The first detailed study of New Zealand species of *Pseudocyphellaria* [as the genus *Sticta*] was that of Babington (1855), based on Hooker's New Zealand collections, supplemented with a wide range of both historical and more recently gathered material including collections of Banks & Solander, Forster, Anderson, Menzies, Allan and Richard Cunningham, Bidwill, W. Stephenson, Samuel Mossman, Everard Home, Richard Taylor, Colenso, Lyall, Monro, and Sinclair, as well as specimens from the Paris herbarium. Babington discussed 25 taxa in some detail, provided a rudimentary infrageneric classification of *Sticta*, and described the following new taxa: *S. colensoi* and var. *pinnatifida* Church. Bab., *S. richardi* var. *glauca* Church. Bab., *S. richardi* var. *rufovirescens* Church. Bab., *S. fragillima* Church. Bab., *S. granulata* Church. Bab., *S. hookeri* Church. Bab., *S. limbata* var. *subflavida* Church. Bab., and *S. montagnei* Church. Bab. The account also provided excellent illustrations (by W. Fitch) of *S. colensoi*, *S. carpoloma*, *S. faveolata*, *S. hookeri*, and *S. coriacea*, and it stands as the major early account of the genus after Delise (1825*a*, 1825*b*), with five of his names still in use today.

For the next 50 years relatively few new taxa referable to *Pseudocyphellaria* were described from New Zealand collections despite extensive literature, viz., Hooker, 1867; Hue, 1890, 1901; Knight, 1871, 1880; Krempelhuber, 1868, 1870, 1876*a*, 1876b, 1881; Lindsay, 1859, 1866, 1867, 1869; Lojka, 1886; Müller Argoviensis, 1883, 1887*a*, 1887*b*, 1894, 1895; Nylander, 1858*a*, 1858*b*, 1860*b*, 1865, 1866, 1868*b*, 1876; Stizenberger, 1889, 1895; Tuckerman, 1874.

Subsequent to Babington's account, new taxa from New Zealand referable to *Pseudocyphellaria* appeared sporadically until the end of the century and included *Sticta fossulata* var. *physciospora* Nyl. (Nylander, 1860*b*); *Sticta subcoriacea* Nyl. [= *P. coriacea*] (Nylander, 1865); *S. episticta* Nyl. (Nylander, 1865); *Stictina fragillima* f. *lutescens* Nyl. [= *P. cinnamomea*] (Nylander, 1866); *Sticta glaucolurida* Nyl. [= *P. carpoloma*], *S. homoeophylla* Nyl., *S. subvariabilis* Nyl. [= *P. multifida*] (Nylander, 1867); *Sticta freycinetii* var. *isidioloma* Nyl. [= *P.*

glabra], *Ricasolia elaphocera* Nyl. [= *P. coriacea*] (Nylander, 1868*b*); *S. urvillei* var. *flavicans* f. *laceratula* Krempelh. [= *P. pickeringii*], *S. freycinetii* var. *stauromatica* Krempelh. [= *P. glabra*], *S. faveolata* f. *angustifolia* Krempelh., nom. nud. [= *P. billardierei*] (Krempelhuber, 1870); *Sticta hirta* Stirton [= *P. coronata*] (Stirton, 1873); *Sticta pickeringii* Tuck. (Tuckerman, 1874); *Sticta fossulata* f. *pallida* Krempelh. [= *P. rufovirescens*] (Krempelhuber, 1876*a*); *S. lividofusca* Krempelh. (Krempelhuber, 1876*b*); *S. canaliculata* Knight [= *P. coriacea*] (Knight, 1877); *S. coronata* Müll. Arg. (Müller Argoviensis, 1879); *S. amphisticta* Knight [= *P. lividofusca*] (Knight, 1880); *S. fossulata* f. *expallida* Krempelh. [= *P. rufovirescens*], *Parmelia isabellina* Krempelh. [= *P. glabra*] (Krempelhuber, 1881); *S. borneti* Müll. Arg. [= *P. carpoloma*] (Müller Argoviensis, 1882); *Stictina fragillima* var. *dissecta* Müll. Arg. [= *P. dissimilis*], *Sticta freycinetii* var. *glabrescens* Müll. Arg. [= *P. glabra*], *S. freycinetii* var. *tenuis* Müll. Arg. [= *P. glabra*] (Müller Argoviensis, 1883); *S. fossulata* var. *subcyphellata* Nyl. [= *P. rufovirescens*] (Nylander, 1888*b*); *Stictina fragillima* f. *sublutescens* Hue [= *P. cinnamomea*] (Hue, 1890); *S. fragillima* var. *myrioloba* Müll. Arg. [= *P. fimbriatoides*], *S. mougeotiana* var. *dissecta* Müll. Arg. [= *P. neglecta*], *Sticta pubescens* Müll. Arg., *S. psilophylla* Müll. Arg. [= *P. chloroleuca*], *S. psilophylla* f. *amphicarpa* Müll. Arg. [= *P. multifida*], *S. amphisticta* var.*platyloba* Müll. Arg. [= *P. lividofusca*] (Müller Argoviensis, 1892); *S. elatior* Stirton [= *P. faveolata*], *S. expansa* Stirton [= *P. carpoloma*], *S. lorifera Stirton* [= *P. faveolata*] (Stirton, 1900).

The last 15 years of the 19th century saw several detailed accounts or lists of New Zealand Lobariaceae in which species of *Pseudocyphellaria* are recorded, viz., Nylander, 1888*b*; Hue, 1890; Müller Argoviensis, 1892, 1894, 1896, most based largely on collections of Charles Knight, William Colenso, and the material from the Hookerian herbarium at Kew, with Hellbom's (1896) account, where many taxa now in *Pseudocyphellaria* are placed in *Lobaria*, detailing lichens collected in New Zealand in 1875–1875 by Sven Berggren. John Buchanan's lichens from Otago and Wellington, and T. W. N. Beckett's collections from Canterbury and the Manawatu were studied by James Stirton in Glasgow (Stirton, 1873, 1875, 1898, 1900), who described several taxa from them referable to *Pseudocyphellaria*.

The major 19th century accounts record the following numbers of taxa of *Pseudocyphellaria*: 11 taxa (Hooker & Taylor, 1844), 24 taxa (Babington, 1855), 34 taxa (Nylander, 1888*b*), 52 taxa (Müller Argoviensis, 1894), and 50 taxa (Hellbom, 1896); however, many of the names recorded in these accounts were synonyms of widespread and polymorphic species. At the close of the 19th century 27 species of *Pseudocyphellaria* accepted today were known from New Zealand: *P. argyracea*, *P. aurata*, *P. billardierei*, *P. carpoloma*, *P. chloroleuca*, *P. cinnamomea*, *P. colensoi*, *P. coriacea*, *P. coronata*, *P. crocata*, *P. dissimilis*, *P. episticta*, *P. faveolata*, *P. glabra*, *P. granulata*, *P. homoeophylla*, *P. hookeri*, *P. intricata*, *P. lividofusca*, *P. montagnei*, *P. multifida*, *P. neglecta*, *P. physciospora*, *P. pickeringii*, *P. pubescens*, *P. rubella*, and *P. rufovirescens*.

The 20th century

In contrast to the taxonomic activity of the late 19th century, the first 40 years of the present century saw very little new work on the New Zealand Lobariaceae apart from the discursive account of Hue (1901) which was mainly a reworking of Nylander-annotated material in Paris, supplemented with collections of Filhol from Campbell I. and New Zealand, H. L. Travers from the Chatham Is and New Zealand, and a few specimens collected by Cockayne from Stewart I. and identified by Lindau (Cockayne, 1910); and Cheel's two bibliographical treatments of South Pacific Lobariaceae (Cheel, 1912, 1914).

The first lichenologist to undertake a comprehensive survey of *Pseudocyphellaria* in the sense of Vainio (1890) was the Uppsala botanist G. E. Du Rietz. In the early 1920s he began serious work on Southern Hemisphere species of *Sticta* and *Pseudocyphellaria* and annotations he made on numerous specimens in H, S, UPS, and W, attest his knowledge of taxa in these genera. However, he published only a brief note on the Southern Hemisphere species *P. freycinetii* and *P. chloroleuca* (Du Rietz, 1924), his use of the latter name being sensu *P. glabra*. He made large collections from New Zealand and Australia in 1925–1926, but these were never worked up for publication, although a few of his New Zealand collections were referred to by Magnusson (1940). Du Rietz was, however, instrumental in encouraging local New Zealand botanists to collect lichens, especially H. H. Allan, the first Director of Botany Division, DSIR. Allan sent New Zealand lichens to Wien to Zahlbruckner, and besides his own extensive gatherings of *Pseudocyphellaria*, specimens from Lucy B. Moore and Lucy M. Cranwell from various North I. localities, and of J. S. Thomson and G. Simpson from South I. habitats were also included. Zahlbruckner's posthumous work *Lichenes Novae Zelandiae* . . . (1941) includes the first major account of New Zealand Lobariaceae since the 19th century (pp. 279–293) with 50 taxa of *Pseudocyphellaria* represented in *Sticta* (sections *Eusticta* and *Stictina*). Among these, Zahlbruckner described the following new taxa: *Sticta condensata* Zahlbr. [= *P. faveolata*], *S. coriacea* f. *vestitula* Zahlbr., [= *P. coriacea*], *S. amplificata* Zahlbr. [= *P. homoeophylla*], *S. variabilis* var. *cinerata* Zahlbr. [= *P. chloroleuca*], and *S. intricata* var. *fimbriata* Zahlbr. [= *P. dissimilis*]. Zahlbruckner had a rather confused idea of some taxa, and in his list of 50 names, only 24 are referable to *Pseudocyphellaria*, now accepted as occurring in New Zealand. He apparently relied on published descriptions or earlier accounts of names reported from New Zealand and obviously examined very few types. For instance, although he correctly identified *P. homoeophylla* in a few cases, he also described *Sticta amplificata* for well-developed specimens of this species, and placed other collections of it under *S. dissimulata*, *S. sinuosa*, and even *S. cinnamomea*. His account is, however, an advance on earlier treatments, for it surveys a much wider range of collections, from North Auckland, the Volcanic Plateau, Mt Egmont, and Wellington in North I., and from Marlborough, Westland, Otago, Southland, and Fiordland in South I. It must also be noted that Zahlbruckner died before a final revision of his manuscript could be made and hence his published account contains a number of errors that may well have been rectified had he lived. For the next 30 years, Zahlbruckner's treatment of taxa referable to *Pseudocyphellaria* strongly influenced succeeding bibliographic, chemical, ecological, and taxonomic accounts, notably Allan (1948, 1949), Martin (1965, 1966, 1968, 1969*a*, 1969*b*), and Martin & Child (1972).

Although species of *Pseudocyphellaria* are amongst the most prominent and widespread of New Zealand's foliose lichens and constitute an appreciable biomass in forest ecosystems, they were largely dismissed (together with bryophytes) from ecological studies until the 1960s. H. H. Allan (1927) appealed for a greater awareness of lower plants in ecological studies 'it is now realised that mosses, lichens, liverworts and fungi are of equal importance with the so-called "higher" plants, and have equally important lessons to teach- economic no less than "purely scientific"' However, apart from a brief reference to lichens from the Antipodes (Cockayne, 1928) and Jablonszky's collections from Waikaremoana (Szatala, 1939), lichens were ignored in floristic and ecological surveys until the posthumous work of Murray (1963) and the influence of P. W. James (in Mark *et al.*, 1964), who curated Murray's lichens (OTA) in 1962–1963.

Floristic and ecological work in which species of *Pseudocyphellaria* are recorded appeared first in Otago (Martin, 1965, 1969*a*, 1969*b*, 1970; Galloway, 1966, 1968*a*, 1968*b*; Mark & Bliss, 1970; Scott, 1970; Scott & Armstrong, 1966; Scott & Rowley, 1975) to be followed by information from Canterbury (Dodge, 1971 [*P. neozelandica* Dodge = *P. colensoi*]; Galloway, 1976, 1978*b*; Jørgensen & Galloway, 1983; Burrows, 1977), Westland (Wardle, 1977; Simpson & Galloway, 1981), and Nelson (Galloway & Simpson, 1978). North I. floristic studies in the 1970s discussed species of *Pseudocyphellaria* from a number of offshore islands (B. W. Hayward, 1973; B. W. & G. C. Hayward, 1974*a*, 1974*b*; 1979, 1980, 1982*a*; 1982*b*; 1983; G. C. & B. W. Hayward, 1973*a*, 1973*b*, 1978; Hayward *et al.*, 1975, 1976, 1981, 1986; Dakin & Galloway, 1980); from the Urewera National Park (see work of Green, and of Snelgar under lichen physiology below); and from Mt Tarawera (Clarkson & Clarkson, 1983). Species of *Pseudocyphellaria* from the subantarctic islands (including the Auckland, Campbell, Macquarie, and Snares groups) are discussed by Dodge (1948), Dodge & Rudolph (1955), Dodge (1971), Fineran (1971), Imshaug [1977– a particularly important and overlooked paper giving a convincing account of the distinction of the closely similar faveolate taxa *P. billardierei* (as *P. flotowiana*), *P. physciospora*, and *P. faveolata*, using anatomical, chemical, and statistical methods], and Filson, 1981*a*, 1981*b*.

Chemical work on New Zealand species of *Pseudocyphellaria* begun by Murray (1952) was continued with great success by Corbett and his students at Otago University, and by Wilkins at Waikato University (see below under Chemistry).

Taxonomic studies on New Zealand *Pseudocyphellaria* undertaken preparatory to the present study include Galloway, 1983*b*, 1985*a*, 1985*b*, 1986*b*; Galloway & James 1977, 1980; Galloway *et al.*, 1983*b*; Hawksworth & Galloway, 1984; and Renner & Galloway, 1982. During these studies the following new taxa were established: *P. allanii* D. Galloway, *P. ardesiaca* D. Galloway, *P. bartlettii* D. Galloway, *P. crassa* D. Galloway, *P. degelii* D. Galloway & P. James, *P. durietzii* D. Galloway, *P. fimbriata* D. Galloway & P. James, *P. fimbriatoides* D. Galloway & P. James, *P. gretae* D. Galloway, *P. knightii* D. Galloway, *P. maculata* D. Galloway, *P. margaretiae* D. Galloway, *P. murrayi* D. Galloway, and *P. sericeofulva* D. Galloway.

Materials and methods

The following account is based on examination of an extensive range of herbarium material as well as collection and examination of material in the field from 1963–1983. Type and representative material was obtained from the following herbaria: ABD, AK, AKU, BM, BP, CANU, CHR, COLO, E, FH, FI, G, GB, GZU, H, H-NYL, L, LD, LINN-SM, M, MANCH, MB, MEL, MSC, NY, OTA, PC-HUE, PC-LENORMAND, PC-MONTAGNE, PC-THURET, S, U, UPS, UPS-THUNBERG, US, VER, W, WELT, WRSL, WU, ZT, and from private herbaria of the following individuals: the late J. K. Bartlett (now in AK), G. Degelius (Askim), J. A. Elix (Canberra), B. W. & G. C. Hayward (Lower Hutt), L. Tibell (Uppsala), and V. Wirth (Stuttgart). A representative range of all taxa discussed in this paper is preserved in BM.

Field studies: With the exception of *P. bartlettii*, *P. haywardiorum*, *P. physciospora*, and *P. sericeofulva*, all of the species discussed below were studied in their natural habitats in order to assess the extent of environmentally induced variation, as well as to determine individual ecological requirements. Field studies ranged from the Three Kings Is (Lat. 34°6′S) to southern Stewart I. (Lat. 48°S). Most of the major geographical regions of New Zealand were surveyed, with the exception of North Auckland, the east coast of North I. and north-west Nelson, Marlborough, and South Westland in South I. The subantarctic islands (Snares, Auckland, Antipodes, Campbell, and Macquarie Is) were not visited, nor were the Chatham Is, although collections from the Auckland, Antipodes, Campbell, Chatham, Macquarie, and Snares Is were examined in the herbarium.

Light microscopy: Observations and measurements of external features were made at × 10 to × 30 with an Olympus stereomicroscope. Anatomical features were investigated with a Leitz Dialux 20 microscope. Sections were cut with a Kryomat freezing microtome giving section thicknesses of 15–20 µm. Sections were normally mounted in water followed by (or directly in) 10% KOH(K), but cotton-blue in lactophenol was also sometimes used. Tests for amyloid reactions were made by mounting directly in Lugol's iodine solution, or in this solution following treatment with 10% K.

Scanning electron microscopy (SEM): Material for SEM was air-dried, attached to aluminium stubs with araldite and sputter-coated using a gold-palladium or a gold target. Stubs were examined in an ISI 60A microscope using back-scatter detection.

Thin-layer chromatography (t.l.c.): Representative samples of all taxa referred to in this study (including all type specimens) were analysed by t.l.c. using standard procedures (Culberson, 1972; Culberson & Johnson, 1976: Culberson *et al.*, 1981; Wilkins & James, 1979; White & James 1985).

Species descriptions are based on type material supplemented with a range of recently collected, characteristic specimens. Details of distinguishing features, variation, chemistry, ecology, and distribution are given for each species together with notes on typification and nomenclature when applicable. All species have distribution maps, though full distribution lists are given only in instances where critical or new taxa are involved.

Abbreviations of describing authors follow Laundon (1979); those of journals to the third (1980) edition of Serial Publications in the British Museum (Natural History) Library; and those of books to Hawksworth (1974) and to Stafleu & Cowan (1976–1986).

Results

Morphology

Species of *Pseudocyphellaria* discussed in this revision are conspicuous, foliose lichens growing on twigs, bark, soil, or rock, often over or amongst bryophytes or other lichens in a wide variety of habitats. Morphological features useful in species delimitation are discussed under subheadings below.

Habit: Thalli of *Pseudocyphellaria* are often very large, (2–)6–20(–50) cm diam.; some of the species found in New Zealand are among the largest of foliose lichens known, orbicular, rosette-forming or irregularly laciniate, subpendulous to ± straplike, and are characterized by scattered pseudocyphellae on the lower surface, occasionally also on the upper surface as well. *Lobes* are very variable in size, shape, and branching, but even so it is possible to distinguish three main morphologies although certain species may show a degree of overlap, depending on local microclimatic and microhabitat parameters. (1) *Monophyllous*: no discernible branching at the apices, with the lobes ± broadly rounded, often compact, and ± rosette-forming, e.g. *P. ardesiaca*, *P. bartlettii*, *P. coronata* (twig forms), *P. crocata*, *P. intricata*, *P. neglecta*, and *P. rubella*. (2) *Dichotomous*: lobes are ± narrow, often also somewhat straplike, and are noticeably dichotomously branched at the apices. Dichotomous branching occurs at an early stage in the growth of the lobe and is clearly visible in even very young plants. Further apical growth of the bifurcating tips may be equal or unequal, and the tips themselves may be ± acute, truncate or rounded. Lobes distal to the developing tips may be smooth, wrinkled or ± faveolate, and variable in width. Dichotomously branching species include: *P. allanii*, *P. billardierei*, *P. carpoloma*, *P. chloroleuca*, *P. cinnamomea*, *P. coriacea*, *P. crassa*, *P. degelii*, *P. dissimilis*, *P. durietzii*, *P. faveolata*, *P. glabra*, *P. homoeophylla*, *P. jamesii*, *P. lindsayi*, *P. lividofusca*, *P. maculata*, *P. murrayi*, *P. physciospora*, *P. pubescens*, *P. rufovirescens*. Species with ± well-defined dichotomous lobe branching are generally rather loosely attached to the substrate and may often be ± hanging. (3) *Complex-imbricate*: no regular discernible branching pattern is visible, often overlapping and crowding of lobes obscures an initial unequal branching pattern. A large proportion of the taxa discussed in this account have this lobe morphology and generally speaking those that do are more closely appressed to the substrate than those having dichotomously branching lobes. Complex-imbricate species include: *P. argyracea*, *P. aurata*, *P. chloroleuca*, *P. colensoi*, *P. corbettii*, *P. coronata*, *P. crocata*, *P. degelii*, *P. dissimilis*, *P. durietzii*, *P. episticta*, *P. fimbriata*, *P. fimbriatoides*, *P. glabra*, *P. granulata*, *P. gretae*, *P. haywardiorum*, *P. homoeophylla*, *P. hookeri*, *P. intricata*, *P. knightii*, *P. lindsayi*, *P. lividofusca*, *P. maculata*, *P. margaretiae*, *P. montagnei*, *P. multifida*, *P. neglecta*, *P. nermula*, *P. physciospora*, *P. pickeringii*, *P. poculifera*, *P. pubescens*, *P. rubella*, *P. sericeofulva*, and *P. wilkinsii*.

The margins of lobes may be entire (e.g. *P. billardierei*, *P. homoeophylla*, *P. physciospora*) or variously notched, incised, pectinate, crenate or ragged (e.g. *P. chloroleuca*, *P. colensoi*, *P. multifida*, *P. pickeringii*, *P. poculifera*) plane to sinuous and ± ascendent, or ± involute, furnished with isidia (e.g. *P. dissimilis*, *P. glabra*), phyllidia (e.g. *P. fimbriata*, *P. neglecta*), or soredia (e.g. *P. aurata*, *P. haywardiorum*, *P. intricata*) in punctiform, erose or labriform soralia, and occasionally with ± conspicuous, linear, punctate or verruciform pseudocyphellae (most notably in *P. carpoloma*, *P. crassa*, *P. faveolata*, *P. margaretiae*, *P. murrayi*, *P. poculifera*, *P. pubescens*, and *P. rubella*). Many species have conspicuously thickened margins, most noticeable on the lower surface as in *P. billardierei* (× 10 lens), but occasionally also on the upper surface as well, the thickening being in the form of a narrow, raised, rounded, ± continuous ridge. Marginal thickening is much less apparent in species having prominent marginal pseudocyphellae (e.g. *P. faveolata*). In *P. crassa* the thick tomentum of the lower surface often appears at the lobe margins as a ± distinct fringe.

Lobes are attached to the substrate either (1) by tomental hyphae over the greater part of the lower surface, or (2) by scattered fascicles or tufts of anchoring hyphae, or (3) directly to the lower cortex in those species with poorly developed tomentum. In *Pseudocyphellaria*, the degree of attachment of thalli to the substrate appears, in certain cases at least, to be determined in part by ecological conditions obtaining at the substrate surface, as does the expression of lobe morphology in some variable species. Light, and moisture appear to be of prime importance, and Snelgar & Green (1981*a*) have shown that populations of *P. dissimilis* from shade, semi-shade, and full sunlight, have different morphologies and varying thicknesses of tomentum on the lower surface. Shade populations are only loosely attached, while well-illuminated populations are closely attached to the substrate with only the lobe tips free. Tomentum is longer and thicker in the sun populations, *c.* four times thicker than in shade populations, and three times thicker than in semi-shade populations. Such differences correlate with the evaporative stress of the different environments, the sun population being most able to resist desiccation by adapting in three ways, viz. (1) the thallus has the classic xerophyte characteristic of reduced surface area to volume ratio, (2) increased water storage capacity is attained by increased thallus thickness and a thicker layer of tomentum, and (3) thalli are more closely appressed to the substrate, thereby aiding water storage by tomental hyphae and reducing the area exposed to water loss by evaporation (Snelgar & Green, 1981a: 409–410).

Colour: Thallus colour is determined by two main factors: the nature of the photobiont, and the degree of exposure of the habitat in which the lichen grows. When moist, thalli with green photobionts are bright lettuce-green to dark olive-green or glaucous-green; species with usnic acid (*P. corbettii*, *P. glabra*, *P. homoeophylla*) are pale yellowish green, the colour intensifying in specimens from habitats exposed to direct sunlight. Thalli with cyanobionts, when moist, vary from purplish blue (*P. ardesiaca*, *P. nermula*, *P. jamesii*) to livid leaden-grey or dark grey-black (e.g. *P. allanii*, *P. hookeri*, *P. knightii*) to brownish or red-black (e.g. *P. crocata*, *P. haywardiorum*, *P. neglecta*). Thallus colour is also influenced in fresh material of yellow-medulla species (e.g. *P. colensoi*, *P. coronata*, *P. degelii*) by pulvinic acid derivatives in the medulla which impart an underlying yellow or golden hue. The colour of dried material, either in the field or on storage in the herbarium, is pale greenish grey or whitish to fawnish, buff, brown or red-brown. Material of *P. gretae* and *P. rubella* is often tinged reddish or pinkish when dry, and on long storage these colours often intensify. *P. coronata* may also be suffused purplish, both in the field and on storage in the herbarium. Plants exposed to sunlight, or from subalpine to high-alpine grassland habitats are often dark red-brown with increased deposition of pigments in the upper cortex (*P. crocata*, *P. maculata*, *P. neglecta*), or may even become superficially blackened (e.g. *P. faveolata*, *P. glabra*).

Texture: Thallus texture may be smooth, matt, dull, shining, or glossy in parts and dull in others, wrinkled or plicate, to shallowly or deeply faveolate (e.g. *P. carpoloma*, *P. billardierei*, *P. faveolata*, *P. physciospora*, *P. rufovirescens*), plane or undulate, with or without isidia, maculae, papillae, phyllidia, pseudocyphellae, pseudoisidia, soredia, or tomentum.

Tomentum: Tomental hairs occur on the upper surface of a number of species (Fig. 1B,D) although only in four do they cover the entire upper surface (*P. gretae*, *P. margaretiae*, *P. pubescens*, *P. rubella*). In other species, hairs are most commonly seen at, or near, lobe apices or margins, or on marginal phyllidia, or at the base of pedicellate apothecia (e.g. in *P. allanii*, *P. aurata*, *P. coriacea*, *P. crassa*, *P. fimbriata*, *P. fimbriatoides*, *P. intricata*, *P. knightii*, *P. poculifera*). Four species (*P. coronata*, *P. jamesii*, *P. nermula*, and *P. sericeofulva*) have tomentum rather patchily developed on the upper surface. In all cases, tomentum is whitish or pale buff and never dark brown, red-brown or blackened as it is when developed on the lower surface. In general, the tomentum of the upper surface is thinner and more delicate than that of the lower surface. Partially tomentose species are often also ± scabrid in parts and in *P. gretae* and *P. pubescens* a scabrid surface is often seen beneath the tomentum. There seems to be a relationship between scabrosity and tomentum and a scabrid upper surface may in fact represent an arrested early stage in the development of tomentum (Galloway, 1986*a*:110).

Scabrosity: A distinctive, ± scabrid-areolate upper surface (× 10 lens) results when the upper cortex becomes roughened-uneven and broken up into a mosaic of minute, shallowly convex areolae (Fig. 1A,C). Scabrosity in New Zealand species of *Pseudocyphellaria* is rather variable in its occurrence, often being best seen at lobe apices and margins, or on the thalline exciple of apothecia (*P. aurata*, *P. colensoi*, *P. poculifera*), and in irregular patches on the upper surface. There are no distinctively scabrid-areolate species in New Zealand analogous to *P. compar*, *P. scabrosa*, or *P. vaccina* from southern South America (Galloway, 1986*a*); however, in a number of taxa both tomentum and a scabrid-areolate cortex occur together (*P. coriacea*, *P. crassa*, *P. fimbriata*, *P. gretae*, *P. margaretiae*, and *P. pubescens*). Taxa with scabrid-areolate lobes (margins, upper surface or thalline exciple) include *P. allanii*, *P. ardesiaca*, *P. aurata*, *P. chloroleuca*, *P. colensoi*, *P. coronata*, *P. crassa*, *P. degelii*, *P. fimbriata*, *P. fimbriatoides*, *P. gretae*, *P. intricata*, *P. margaretiae*, *P. nermula*, *P. pickeringii*, *P. poculifera*, and *P. pubescens*.

Faveolae: These are shallow to deep depressions, usually smoothly concave, formed between a ± reticulate pattern of interconnecting ridges which may be broad to narrow, smoothly rounded to ± abruptly and sharply defined (Fig. 2). Faveolae are especially characteristic of many taxa in *Pseudocyphellaria*, being more common in narrow-lobed, ± dichotomously branching species than in broad-lobed species. The following faveolate species are known from New Zealand: *P. bartlettii*, *P. billardierei*, *P. carpoloma*, *P. chloroleuca*, *P. colensoi*, *P. coronata*, *P. crassa*, *P. crocata*, *P. degelii*, *P. durietzii*, *P. faveolata*, *P. granulata*, *P. hookeri*, *P. intricata*, *P. jamesii*, *P. maculata*, *P. montagnei*, *P. murrayi*, *P. neglecta*, *P. physciospora*, *P. pickeringii*, *P. pubescens*, and *P. rufovirescens*. Green *et al.* (1985:68, tab. 3) on the basis of experiments

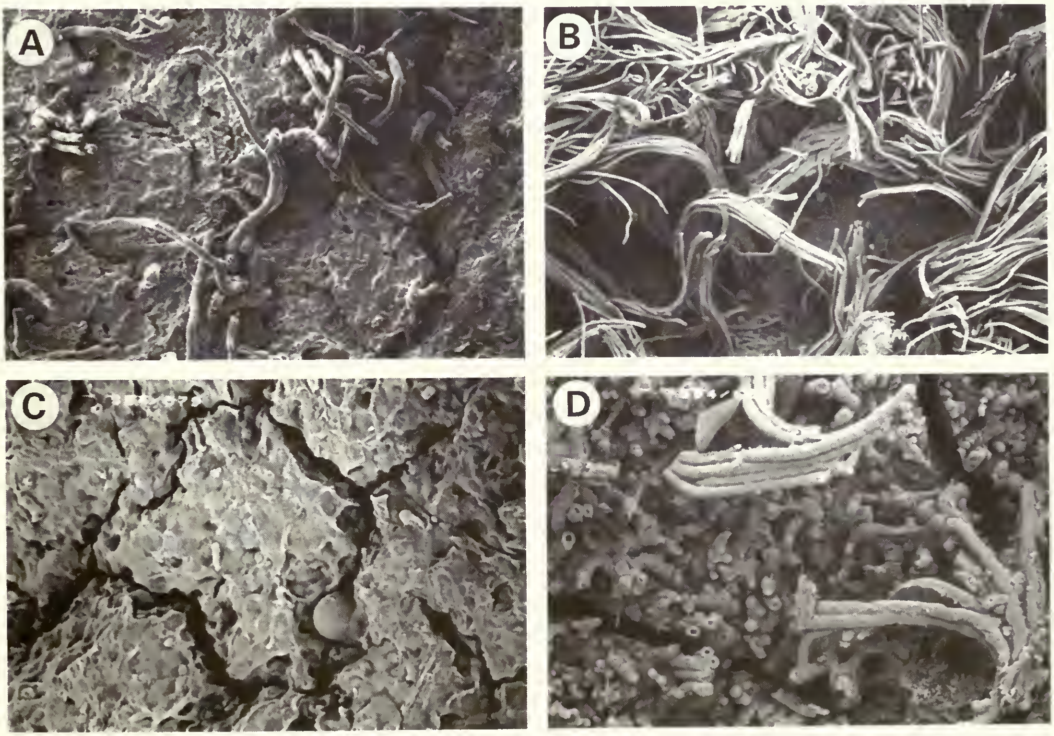


Fig. 1 Scabrosity and tomentum of upper surface. A. *Pseudocyphellaria allanii* × 400. B. *P. margaretiae* × 200. C. *P. nermula* × 500. D. *P. rubella* × 500.

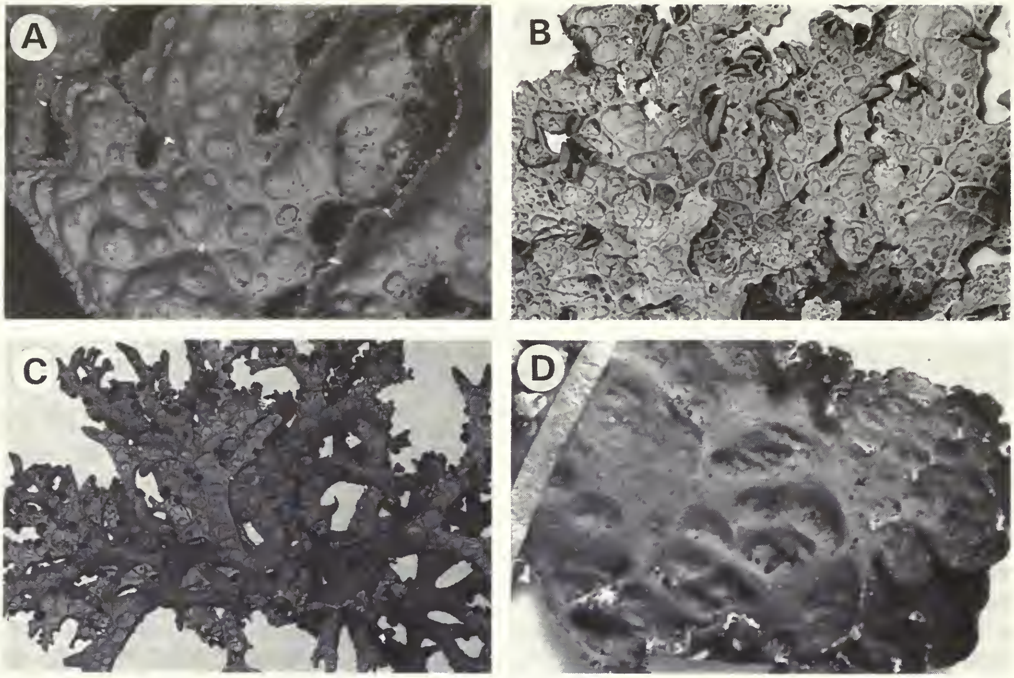


Fig. 2 Faveolae on upper surface. A. *Pseudocyphellaria crassa*. B. *P. durietzii*. C. *P. faveolata*. D. *P. haywardiorum*.

with *P. rufovirescens* [cited as *P. billardierei*] suggest that faveolae of the upper surface may serve as reservoirs to increase external water storage.

Papillae: Papillae are minute, pale, usually hemispherical swellings in the upper cortex (Fig. 3) which are not cephalodia, pycnidia or apothecial initials (use × 10 lens). Their occurrence is spasmodic and varies from sparse to frequent. They are commonly seen in *P. cinnamomea* and *P. dissimilis*, but are also known from *P. corbettii*, *P. fimbriatoides*, *P. glabra*, *P. knightii*, *P. multifida*, and *P. wilkinsii*.

Maculae: Maculae are macroscopic (× 10 lens) photobiont-free, spots or lines visible on the upper surface of certain species as pale white or yellow areas, corresponding to discontinuities in the photobiont layer and imparting a characteristic marbled appearance to the upper surface. The spots or lines which may be arranged in a ± reticulate pattern are best seen in moist thalli and are often more apparent towards the lobe margins than elsewhere on the surface. Maculae are most often found in taxa with *Nostoc* as photobiont, e.g. *P. ardesiaca*, *P. bartlettii*, *P.*

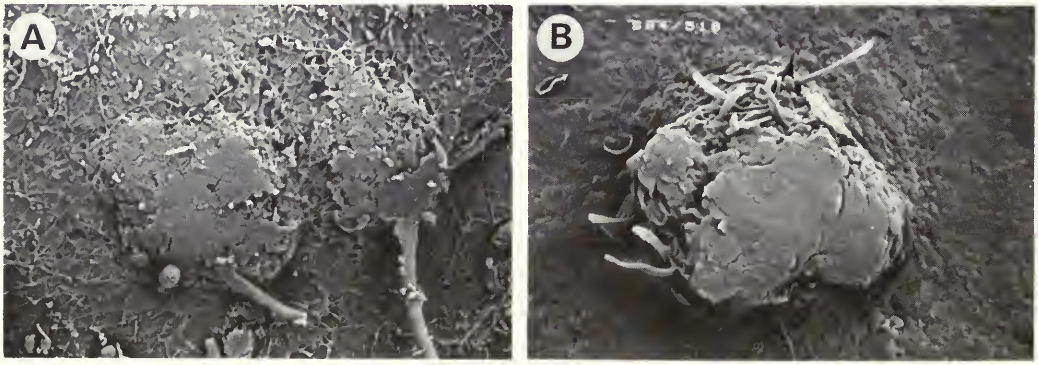


Fig. 3 Papillae on upper surface. A. *Pseudocyphellaria cinnamomea* × 500. B. *P. fimbriatoides* × 500.

cinnamomea, *P. crocata*, *P. dissimilis*, *P. hookeri*, *P. intricata*, *P. jamesii*, *P. knightii*, *P. maculata*, *P. murrayi*, *P nermula*, and *P. sericeofulva*. Occasionally they occur in species with a green photobiont such as *P. degelii* and *P. glabra*, though they are much less common than in species with cyanobionts. Certain species, e.g. *P. dissimilis*, sometimes develop extensive photobiont-free patches, though the cause of these often extensive local decolorizations of the photobiont cells is at present unknown.

Pseudocyphellae: These are pores in cortical tissue which are usually smaller and less differentiated than cyphellae (Hale, 1981; Lawrey, 1984). Their occurrence on the lower surface is a major feature of species of *Pseudocyphellaria*, although in a few taxa they may be rare or absent (e.g. *P. dubia*, *P. berteroana*, *P. episticta*) and in others they may in addition be present on the upper surface or at the margins. The development of pseudocyphellae is discussed by Hale (1981) and Lawrey (1984). Pseudocyphellae being plugged with medullary hyphae (Fig. 4),

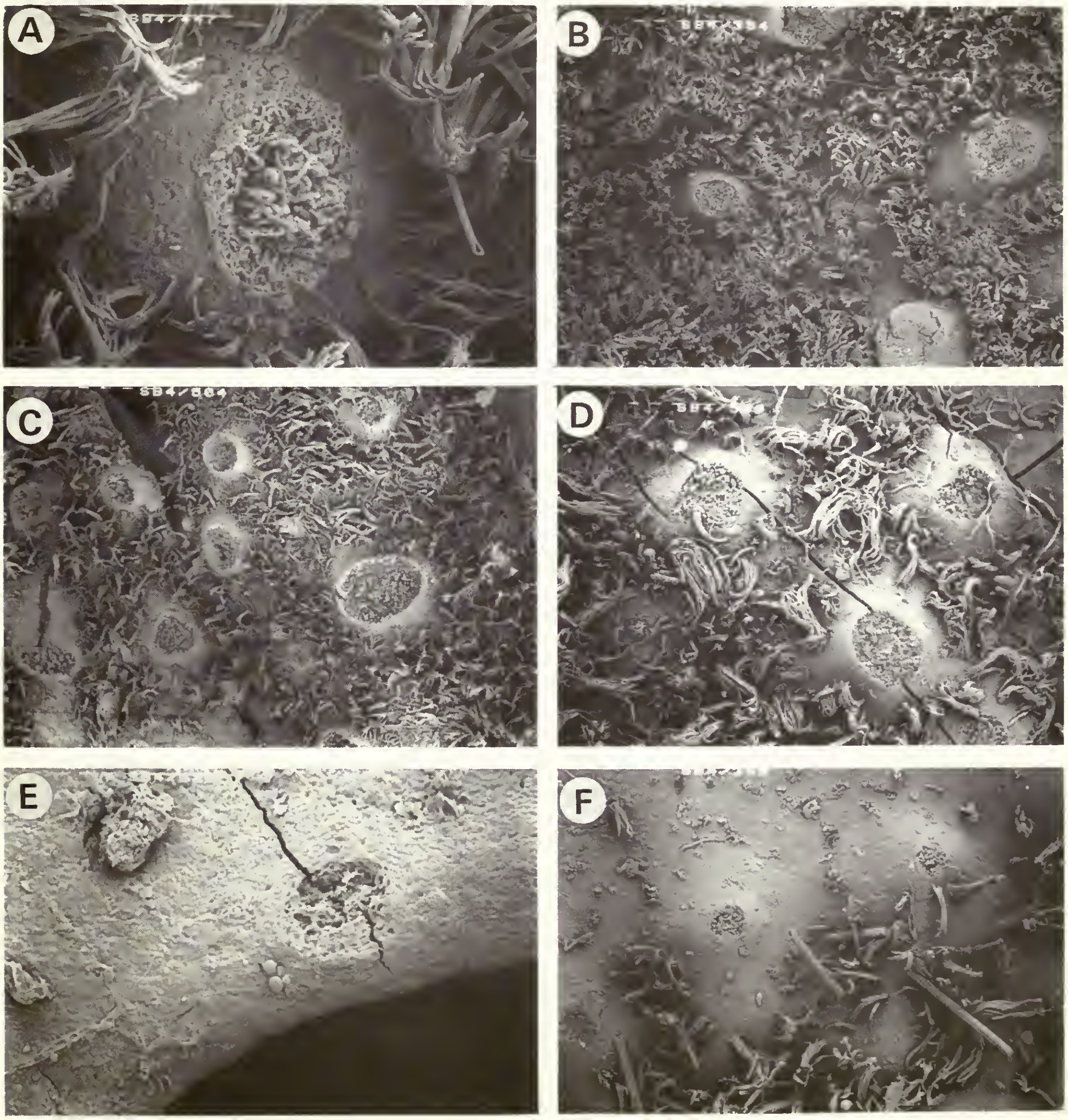


Fig. 4 Pseudocyphellae on lower surface. A. *Pseudocyphellaria crassa* × 200. B. *P. faveolata* × 50. C. *P. fimbriata* × 30. D. *P. lividofusca* × 50. E. *P. multifida* × 250. F. *P. physciospora* × 95.

provide a pathway for diffusion of oxygen and carbon dioxide from both upper and lower lichen surfaces to the interior and have, as well as cyphellae, been implicated in processes of gas exchange (see Henssen & Jahns, 1973; Rundel *et al.*, 1979; Hale, 1981; Green *et al.*, 1985), although this was only proved conclusively for cyphellae (Green *et al.*, 1981). Hale (1981) suggests that gas exchange structures such as pseudocyphellae evolved to overcome the cortical resistances to gas diffusion in large foliose thalli with lobes 5–20 mm wide. However, of the 48 species of *Pseudocyphellaria* in New Zealand, only six have pseudocyphellae on the upper surface, and of the remainder many reach a very large size with lobes in excess of 20 mm wide, so either gas exchange must occur through the upper cortex of these species or else, and much more likely, gas exchange is facilitated by pseudocyphellae at the lobe margins and on the lower surface. Green *et al.* (1981) monitored carbon dioxide exchange in *Sticta latifrons* using a split chamber which allowed separate analysis of gas exchange at the upper and lower surfaces of the thallus. Their results showed that carbon dioxide exchange occurred largely through the lower surface, providing strong circumstantial evidence for the notion that cyphellae have a central role in carbon dioxide uptake during photosynthesis and oxygen uptake during respiration. It is likely that similar results would be obtained with large species of *Pseudocyphellaria*. More recently, Green *et al.* (1985) have suggested that pore systems (cyphellae and pseudocyphellae) in members of the Lobariaceae have three possible adaptations which are of advantage to the lichen system: (1) recycling of respired carbon dioxide (from both photobiont and mycobiont), (2) maintaining a moist internal atmosphere and insulating cells of the photobiont from external drying, and (3) surface water storage. Since pore systems confine carbon dioxide exchange to a small proportion of the thallus surface, liquid water can then be stored over the remainder of the surface without affecting carbon dioxide diffusion.

Pseudocyphellae are found on the upper surface of six species: *P. argyracea*, *P. episticta*, *P. knightii*, *P. lindsayi*, *P. lividofusca*, and *P. wilkinsii* (Fig. 5), and are verruciform, margins raised or not, round, ellipsoid to ± linear, to irregular, ± ulcerose, and becoming sorediate-pseudoisidiate in *P. argyracea* (Fig. 6A) or surrounded by fragile isidia in *P. wilkinsii* (Fig. 6B).

Pseudocyphellae are present on the lower surface of all species of *Pseudocyphellaria* investigated in this study, although in a few cases (e.g. *P. intricata*, *P. episticta*, *P. montagnei*, *P. wilkinsii*) they may be ± inapparent or only very occasionally produced, and then are often most readily seen at or near lobe margins. They are very variable in morphology and also in occurrence, being widely scattered to ± crowded. Generally pseudocyphellae are smaller at the margins and larger centrally, ranging in size from 0·1–2(–2·5) mm diam., in shape from round to sigmoid, irregular to ± linear. The decorticate area which may be flat, concave or convex, is either yellow or white. Pseudocyphellae are either flat and ± flecklike as in *P. chloroleuca*, *P. cinnamomea*, *P. dissimilis*, *P. multifida*, and *P. rufovirescens*, deeply urceolate, starkly white, and often with raised, narrow to ± inapparent margins as in *P. coriacea*, punctiform to verruciform to large-ulcerose with a prominent coarsely granular decorticate area as in *P. intricata*, to ± conical, verruciform-papillate to ± pulverulent, or even pin-prick-like (*P. bartlettii*). In some taxa pseudocyphellae have noticeable margins (× 10 lens) which may be thin to thick, smooth and ± glossy to matt and ± puckered. Species with prominent marginal pseudocyphellae include *P. carpoloma*, *P. crassa*, *P. faveolata*, *P. maculata*, *P. margaretiae*, *P. murrayi*, *P. pubescens*, and *P. rubella*, and the pseudocyphellae range from scattered to numerous, ± prominent and conical-verruciform to punctiform or short-linear.

Deposition of the yellow pulvinic acid derivatives (calycin, pulvinic acid, pulvinic dilactone) in the exposed hyphae of pseudocyphellae is a good taxonomic character and one often used for the separation of related species (e.g. *P. carpoloma* and *P. faveolata*). In some cases (e.g. in *P. physciospora*) the amount of yellow pigment present may be small and this, together with the sometimes small decorticate area of pseudocyphellae, may necessitate a careful examination of pseudocyphellae with a strong lens (×10–×20). In a small number of species with yellow pseudocyphellae, pigment deficient individuals may sometimes be found as reported for the South American species *P. hirsuta* and *P. vaccina* (Galloway, 1986*a*: 109). The following New Zealand taxa have yellow pseudocyphellae: *Pseudocyphellaria ardesiaca*, *P. aurata*, *P. carpoloma*, *P. colensoi*, *P. coronata*, *P. crassa*, *P. crocata*, *P. degelii*, *P. jamesii*, *P. maculata*, *P.*

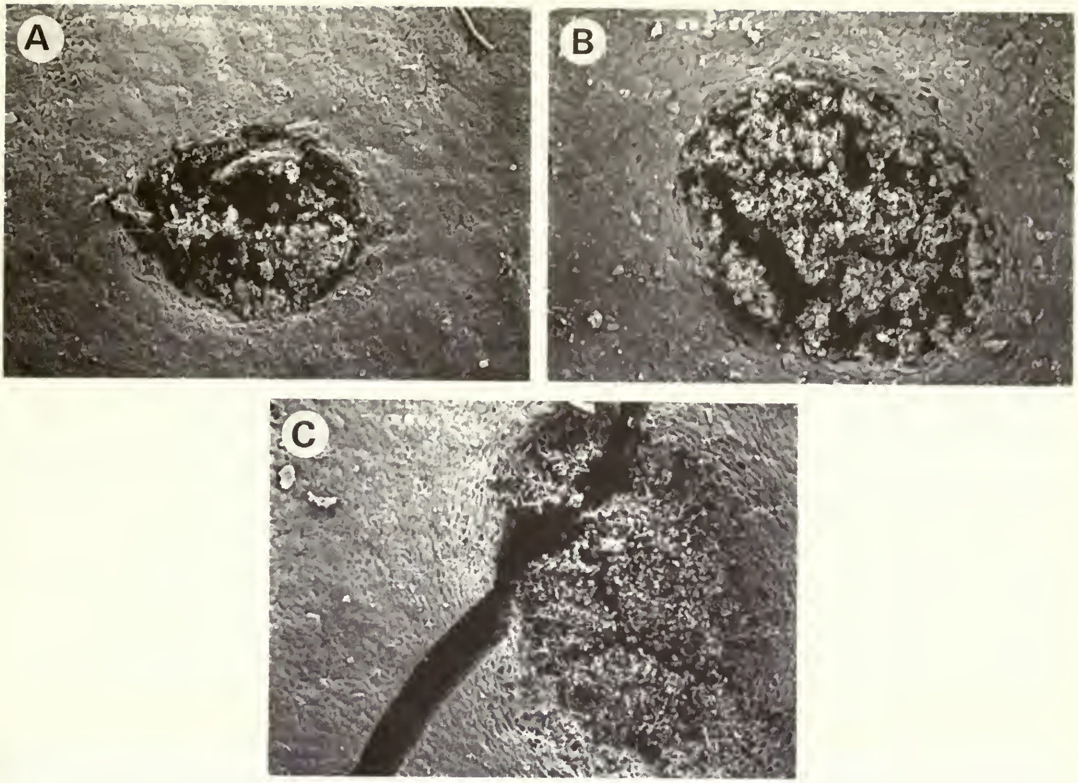


Fig. 5 Pseudocyphellae on upper surface. A. *Pseudocyphellaria knightii* × 300. B. *P. lindsayi* × 400. C. *P. lividofusca* × 300.

margaretiae, *P. nermula*, *P. neglecta*, *P. physciospora*, *P. pickeringii*, *P. poculifera*, *P. pubescens*, *P. rubella*, and *P. sericeofulva*.

Lower surface: The lower surface, which may be smooth, wrinkled, ridged to ± bullate, is thinly to densely tomentose, velvety-pubescent or ± glabrous and some species show all degrees of hairiness from ± glabrous to densely and uniformly tomentose. Tomental hairs are strands of hyphae (often in fascicles of 2–12 or more) which originate from the outermost cells of the lower cortex and which anchor the thallus to the substrate. As Snelgar & Green (1981*a*) have shown,

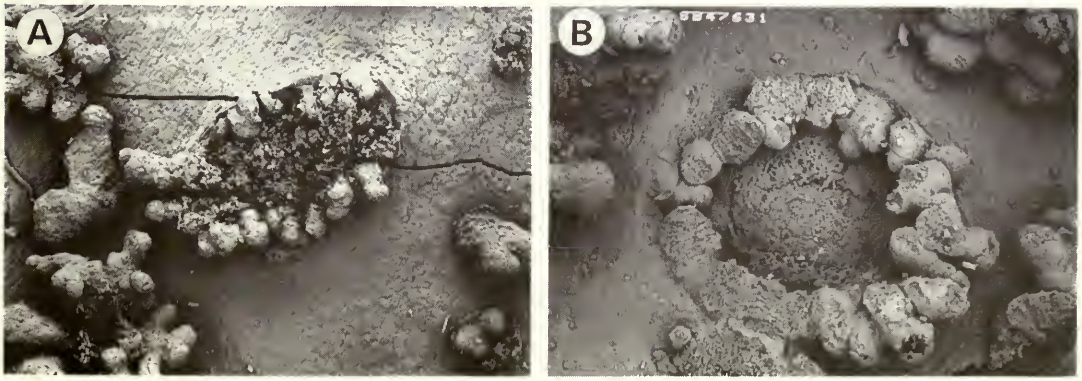


Fig. 6 Pseudocyphellae associated with isidia-pseudoisidia on upper surface. A. *Pseudocyphellaria argyracea* × 100. B. *P. wilkinsii* × 100.

the thickness of the tomentum of the lower surface in different populations is governed by the evaporative demand of their environments, with populations exposed to full sunlight being more closely appressed to the substrate and having a thicker tomentum, and hence increased water storage capacity.

Species with a ± consistently glabrous lower surface include *P. chloroleuca*, *P. rufovirescens*, and *P. glabra*, although occasionally patchily tomentose specimens are found in all three species. Tomentum varies in density from velvety-pubescent (e.g. in *P. haywardiorum*) to thick and woolly or shaggy (*P. crassa*) and may be uniform from margins to centre, or thickly developed centrally with a ± wide, glabrous, smooth or wrinkled, glossy or matt, pale to dark brown or black marginal zone. In *P. dissimilis* and *P. cinnamomea* (occasionally also in *P. multifida*) tomentum is restricted to a narrow, central, raised, somewhat prominent midrib.

Isidia: These are terete in cross-section and are small outgrowths of the thallus and as such have a true cortex, internal to which is a photobiont layer and a central medulla. Isidia may be simple, ± fingerlike, to coralloid-branched, rarely granular-verruciform (Fig. 7) and scattered randomly over the thallus surface, to ± clustered at the margins, or associated with breaks in the thallus surface (*P. chloroleuca*, *P. dissimilis*, *P. glabra*), or occasionally with pseudocyphellae (*P. argyracea*, *P. wilkinsii*), and sometimes thickly covering the upper surface as a diffract crust. Isidia are also sometimes present on the margins and thalline exciple of apothecia. Isidia are vegetative propagules and as such may be ± easily abraded by water, wind, foraging insects, and molluscs, and possibly by birds and other animals. On removal of isidia from the thallus, small pits are left on the surface which, however, should not be confused with pseudocyphellae. Isidia may become eroded-sorediate in *P. argyracea* and *P. poculifera*, or ± phyllidiate as in *P. colensoi*, *P. dissimilis*, *P. gretae*, and *P. pickeringii.*

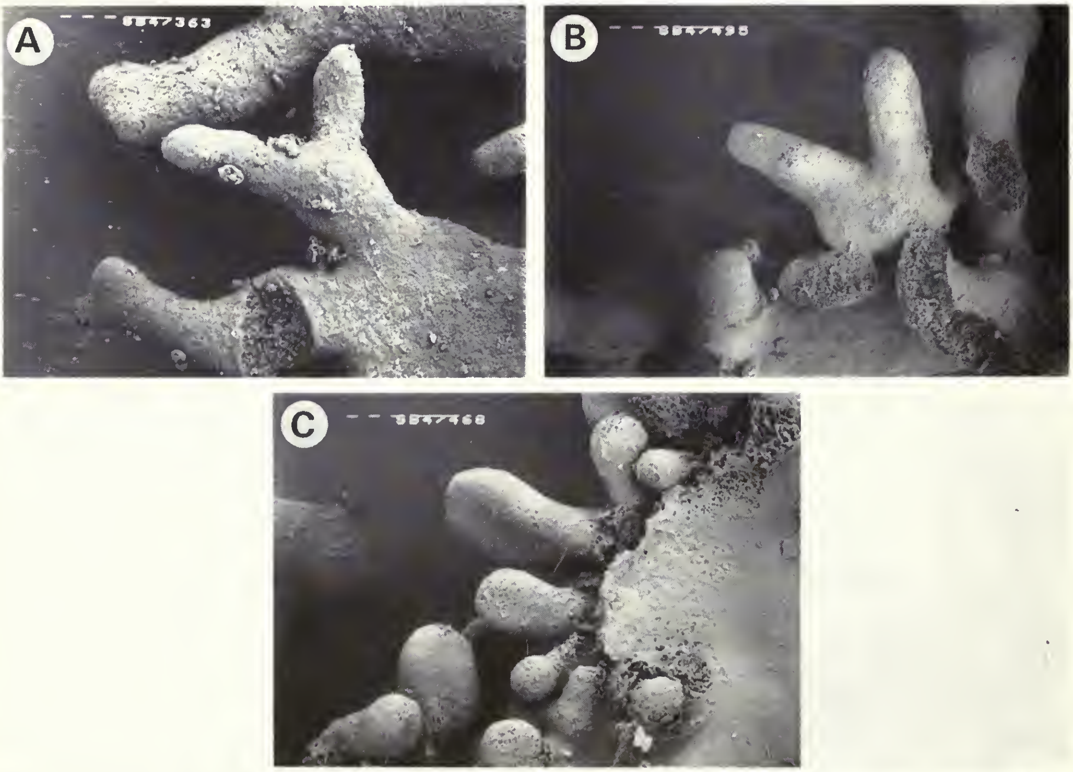


Fig. 7 Marginal isidia on upper surface. A. *Pseudocyphellaria chloroleuca* × 100. B. *P. episticta* × 100. C. *P. glabra* × 100.

Isidia are formed in *P. argyracea*, *P. chloroleuca*, *P. colensoi*, *P. dissimilis*, *P. glabra*, *P. gretae*, *P. pickeringii*, *P. poculifera*, and *P. wilkinsii.*

Pseudoisidia: These are small, delicate, terete, style-formed, simple to coralloid structures, often somewhat darkened and eroding with age, usually 1 mm tall or less and to 0·1 mm diam., often developed at margins of pseudocyphellae (Fig. 6A) on the upper surface (in *P. argyracea*), or at margins of clustered to ± erose soralia. In section, pseudoisidia are ± continuously thinly corticate at first, the entire structure being covered by 1–2 rows of pigmented cortical cells. This cortical covering is generally thinner then the normal cortex elsewhere in the thallus, and is readily abraded at the base of the pseudoisidia on aging, with the formation of efflorescent hyphal masses intermixed with intact tips of pseudoisidia. A feature of pseudoisidia is their ability to reform, at least in part, a new cortex in sorediate areas. Indeed, pseudoisidia often start off as soredia and then become secondarily, partially thinly corticate.

Unlike true isidia, pseudoisidia in *Pseudocyphellaria* appear not to contain photobiont cells below the thinly developed cortical layer. Pseudoisidia are most commonly developed in *P. argyracea* and *P. poculifera*, and are also occasionally found associated with soralia in *P. ardesiaca*, *P. bartlettii*, *P. crocata*, *P. granulata*, *P. haywardiorum*, and *P. intricata*. A detailed discussion of pseudoisidia in several other lichen genera is given in Walker (1985: 11).

Phyllidia: Phyllidia (Fig. 8A–D) are thallus outgrowths similar to isidia and like them, organs of vegetative dispersal. They are distinctly foliose, flattened, dorsiventral structures, usually constricted at the base, simple, expanded at tips, to subcoralloid-palmate or ± pectinate, squamiform to richly divided, or ± straplike. As in the parent thallus they have a distinct upper surface with photobiont layer, and a pale lower surface often with rudimentary tomentum and pseudocyphellae. In two species (*P. fimbriata*, *P. fimbriatoides*) phyllidia have minute,

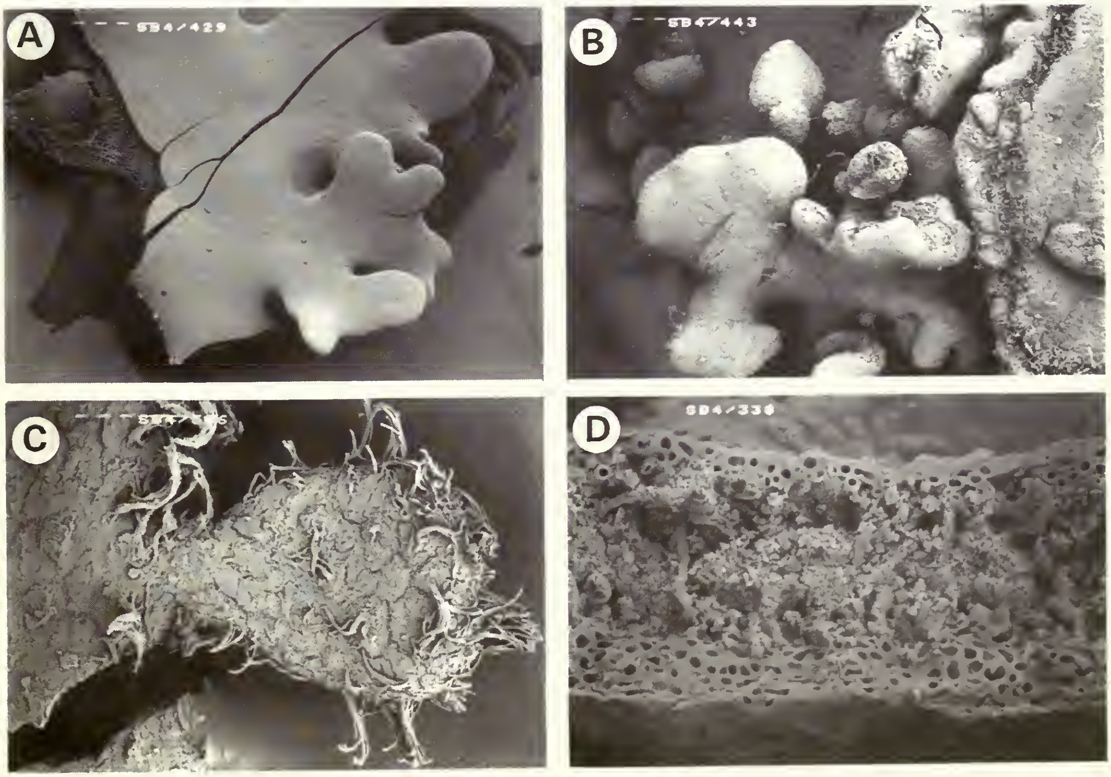


Fig. 8 Phyllidia on upper surface. A. *Pseudocyphellaria corbettii* × 25. B. *P. coronata* × 50. C. *P. fimbriata* × 100. D. *P. montagnei* × 1000 (cross section).

marginal, glistening hairs (Fig. 8C) while those of *P. gretae* are densely and uniformly tomentose. Phyllidia often cluster at lobe margins but are also found laminally especially along breaks in the thallus; they are also developed on the thalline exciple of *P. montagnei*, *P. colensoi*, and *P. coronata* (Fig. 8B). Phyllidia are known from *P. corbettii*, *P. colensoi*, *P. coronata*, *P. dissimilis*, *P. episticta*, *P. fimbriata*, *P. fimbriatoides*, *P. gretae*, *P. montagnei*, *P. multifida*, *P. nermula*, *P. neglecta*, and *P. wilkinsii.*

Soredia: Soredia are present in 10 species: *P. ardesiaca*, *P. argyracea*, *P. aurata*, *P. bartlettii*, *P. crocata*, *P. granulata*, *P. haywardiorum*, *P. intricata*, *P. poculifera*, and *P. rubella*, and are developed on the lobe margins and/or scattered over the upper surface in erumpent, pustular to ± erose, rounded or irregular to ± linear soralia. Marginal soralia may be punctiform to ± linear, or distinctly labriform and eroding areas of the lower surface (in *P. aurata*). Laminal soralia are punctiform, pulverulent to erose, 0·1–3 mm diam., round to irregular, solitary to confluent, sometimes forming reticulate patterns on thallus ridges (e.g. in *P. crocata*, *P. granulata*, *P. intricata*), or obscuring large areas of the upper surface (*P. bartlettii*, *P. granulata*). Soredia are yellow, white, olive-greenish to somewhat blackened, farinose to coarsely granular, gnarled-glomerulate (*P. ardesiaca*), to pseudoisidiate (*P. aurata*, *P. crocata*, *P. intricata*). Occasionally in *P. aurata* and *P. crocata* (especially from humid habitats on *Leptospermum*) development of minute, corticate, cochleate lobes from granular soredia may be seen.

Of the 10 sorediate species present in New Zealand all, except *P. ardesiaca*, *P. argyracea*, and *P. bartlettii*, are known fertile and are not sorediate clones or forms of a non-sorediate fertile parent species (for discussion of sorediate clones see Tehler, 1982). *Pseudocyphellaria granulata* is the sorediate counterpart of *P. faveolata*, the two taxa constituting a species pair and it is possible that *P. ardesiaca* is the sorediate counterpart of *P. jamesii.*

Ascomata: All species studied except *P. allanii*, *P. ardesiaca*, *P. bartlettii*, *P. jamesii*, *P. margaretiae*, *P. nermula*, and *P. sericeofulva* are known fertile, although as a general rule species with soredia only rarely produce ascomata. Two main types of ascomata are found in *Pseudocyphellaria*: (1) Sessile, laminal, or marginal apothecia with a ± well-developed and often scabrid-areolate-verrucose *excipulum proprium* lacking photobiont cells and often appearing ± translucent when wet, characteristic of *P. billardierei*, *P. carpoloma*, *P. chloroleuca*, *P. cinnamomea*, *P. coriacea*, *P. crassa*, *P. degelii*, *P. dissimilis*, *P. episticta*, *P. faveolata*, *P. fimbriata*, *P. fimbriatoides*, *P. glabra*, *P. granulata*, *P. haywardiorum*, *P. homoeophylla*, *P. intricata*, *P. knightii*, *P. lindsayi*, *P. lividofusca*, *P. maculata*, *P. multifida*, *P. murrayi*, *P. neglecta*, *P. pickeringii*, *P. rufovirescens*, and *P. wilkinsii*, (2) ± Pedicellate marginal or submarginal apothecia having a smooth to verrucose-areolate to ± tomentose *excipulum thallinum* containing photobiont cells, found in *P. aurata*, *P. colensoi*, *P. coronata*, *P. durietzii*, *P. gretae*, *P. hookeri*, *P. montagnei*, *P. physciospora*, *P. poculifera*, *P. pubescens*, and *P. rubella.*

Apothecia are nodular-papillate at first with ± prominent, smooth to verrucose-scabrid margins (pale whitish to red-brown) and frequently a plug of sterile tissue or a thick membrane obscures the disc in early stages of its development (Fig. 9C). The disc is often deeply cupuliform, concave at first, and expands at maturity to become plane or convex-undulate; the surface is matt or shining, pale yellow-brown to dark red-brown to brown-black (the colour darker in dried specimens), smooth to ± roughened-papillate and in *P. faveolata*, *P. granulata*, and *P. pubescens* white-pruinose (Fig. 9A,B), the disc appearing greyish or grey-blue, the pruinosity often best developed in young fruits and disappearing with age. Margins may be entire, crenate, dentate-striate, isidiate, sorediate to ± eroded and exposing medullary hyphae, scabrid, phyllidiate, pubescent, tomentose or ± excluded. The exciple is smooth, glossy, or matt to ± tomentose, isidiate or phyllidiate, frequently scabrid-verrucose, pale flesh-pink, buff or red-brown, usually ± translucent when wet (Fig. 9D).

Anatomy

Details of anatomical structure of thalline and apothecial tissues in *Pseudocyphellaria* are discussed in some detail by Hue (1901), Magnusson (1940), and Galloway (1986*a*). *Thalli* of all

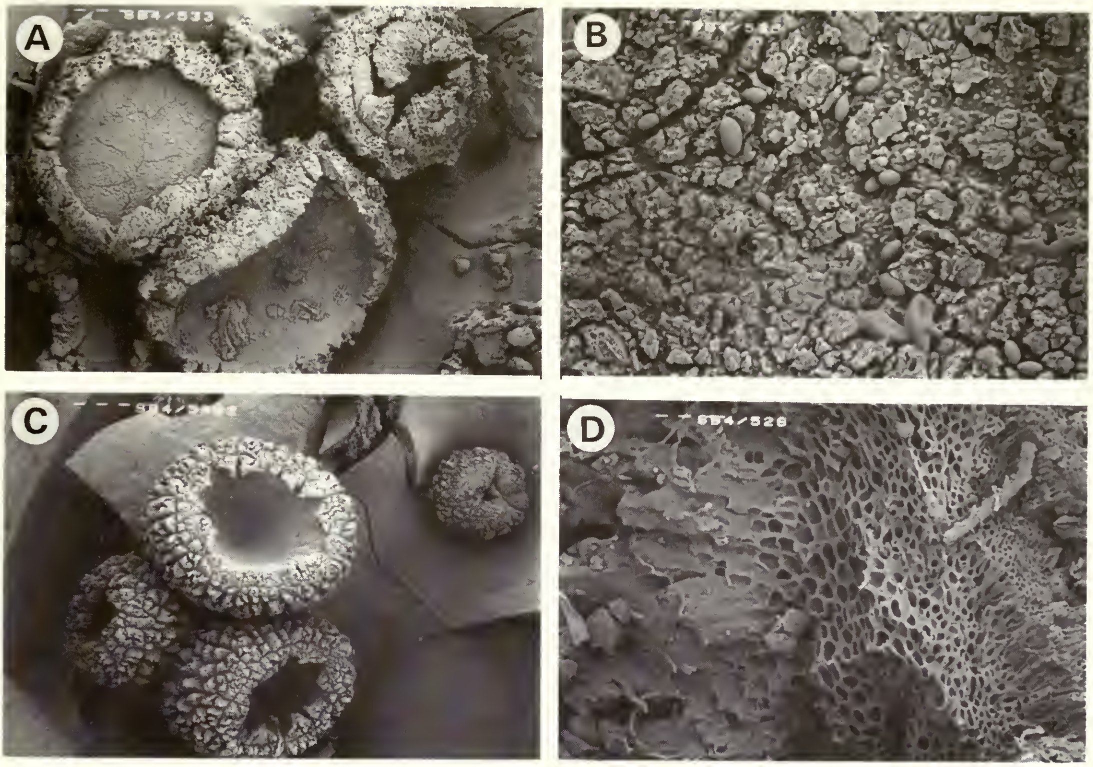


Fig. 9 Ascomatal structures. A. *Pseudocyphellaria granulata*; young, hemiangiocarpic (right) and mature (left) ascomata with pruinose discs × 30. B. *P. granulata*; surface of disc with pruina and ascospores × 500. C. *P. pickeringii*; young, hemiangiocarpic (right) and mature (left) ascomata × 30. D. *P. degelii*; excipular tissue × 500.

species of *Pseudocyphellaria* are heteromerous and between 130–450 μm in thickness, with well-developed specimens (e.g. *P. coriacea*) to 750 μm. Thallus thickness varies considerably within species (particularly in species with ± well-developed faveolae and interconnecting ridges) and is mainly a consequence of the variation in thickness of the medulla and photobiont layer (and to a lesser extent of the upper cortex) dependent on thallus age, and microecological conditions obtaining at the thallus surface. All species have an upper and lower cortex, generally of similar anatomical structure (Fig. 10), though the lower cortex (occasionally also the upper cortex) is normally obscured by the development of tomental hairs from the outermost layer of cortical cells.

Upper cortex: The upper cortex in all species is a paraplectenchyma (pseudoparenchyma) of anticlinally arranged, round to irregular, ± isodiametric, ± angularly thickened cells (4·5–)7–15·5(–18) μm diam., with outermost cells rather smaller, ± compressed, and with somewhat thicker walls than the larger, more loosely arranged cells adjacent to the photobiont layer. Cell wall thickness is within the range 1·5–3·5 μm, with lumina round to irregular 2·5–4·4(–11) μm diam. Cortical cells vary in colour from ± hyaline to pale straw-yellow to orange-brown or red-brown, the colour being most intense at the upper surface and palest close to the photobiont layer. Thickness of the cortex varies from 18–102 μm, but within each species the variation is much less, 4–12(–32) μm. Scanning electron micrographs of the upper surface show the outlines of individual hyphae comprising the underlying tissue, and occasional small, rather irregular pores are seen (Fig. 11). In certain species tomental hairs may develop from cells of the upper cortex (e.g. in *P. gretae*, *P. pubescens*) or the upper cortex is roughened-uneven, appearing areolate-scabrid (Fig. 1A–D).

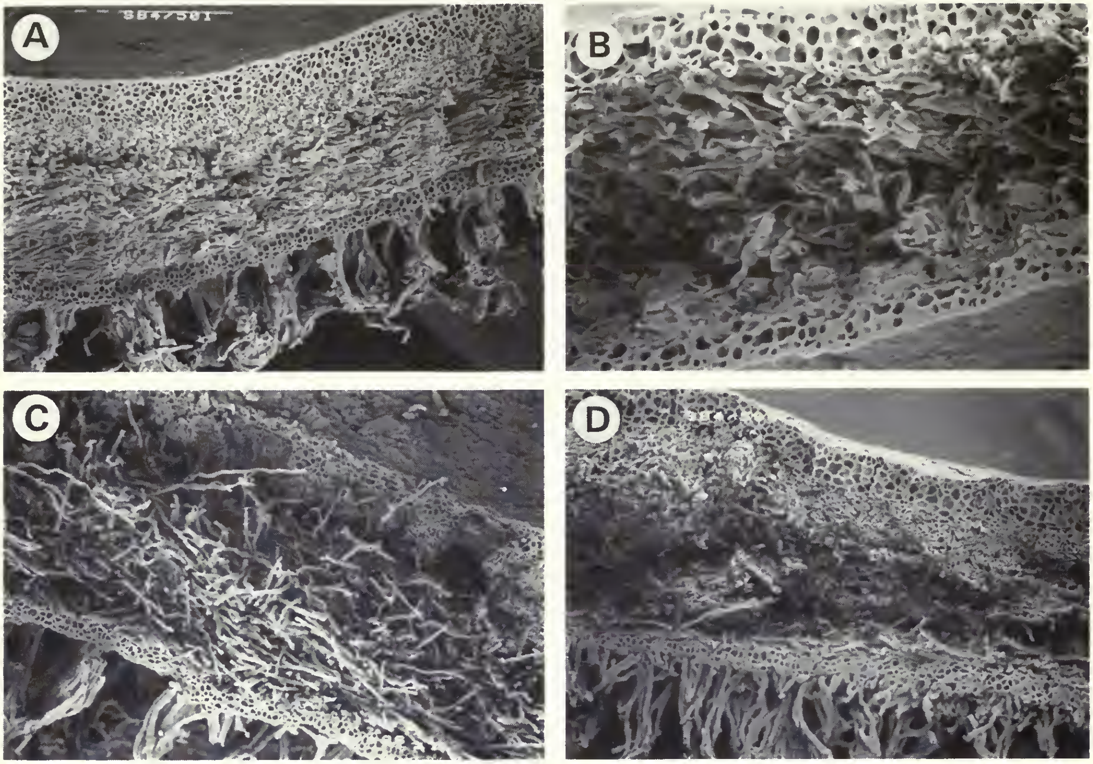


Fig. 10 Cross sections of thalli showing upper and lower cortices, medullary tissue, and tomentum of lower surface. A. *Pseudocyphellaria episticta* × 200. B. *P. fimbriatoides*, lobe margin × 800. C. *P. intricata* × 200. D. *P. nermula* × 200.

Photobiont layer: The photobiont layer lies between the upper cortex and the medulla and varies considerably in thickness, between 11–140 μm, with a majority of taxa having a photobiont layer from 25–50 μm thick. Hyphae of similar structure to those found in the medulla (though sometimes rather thicker), ramify throughout the photobiont cells. Species with a green photobiont have the photobiont cells arranged in a continuous layer, while taxa with a cyanobiont may have a ± continuous layer of photosynthetic cells, or the cyanobiont may be present in discrete clusters or clumps with bands of hyphae separating the photosynthetic tissue. Such discontinuities in the cyanobiont layer are visible macroscopically (× 10 lens) as *maculae*. Thickness of the photobiont layer may vary within species and in certain taxa may even be environmentally controlled; Snelgar & Green (1981*a*), for example, recording that populations of *P. dissimilis* from sunny situations had a thicker cyanobiont layer (50 ± 4 μm) than semi-shaded (48 ± 1 μm), and deeply shaded (38 ± 1 μm) populations of the same species.

Photobionts in *Pseudocyphellaria* are either green algae or cyanobacteria. The cyanobiont in all cases appears to be *Nostoc*, both as primary photosynthetic symbiont and in cephalodia, while green photobionts in the genus are *Chlorella*-like (E. Tschermak-Woess, pers. comm.) or *Dictyochloropsis* (Tschermak-Woess, 1984). The photobiont in New Zealand populations of *Pseudocyphellaria aurata* is *Dictyochloropsis symbiontica* var. *symbiontica*, while other species of *Pseudocyophellaria* examined (*P. fimbriata*, *P. gretae*, *P. homoeophylla*) have an undescribed species of *Dictyochloropsis* as symbiont (Tschermak-Woess, 1984).

Green photobionts and cyanobionts are readily distinguished macroscopically (× 10 lens) in dried and herbarium material. Green photobionts appear either bright green, greenish-yellow or ± colourless when the upper cortex is dissected from the underlying medulla to expose the photobiont layer (seen also when the thallus is cracked or torn), whereas cyanobionts always

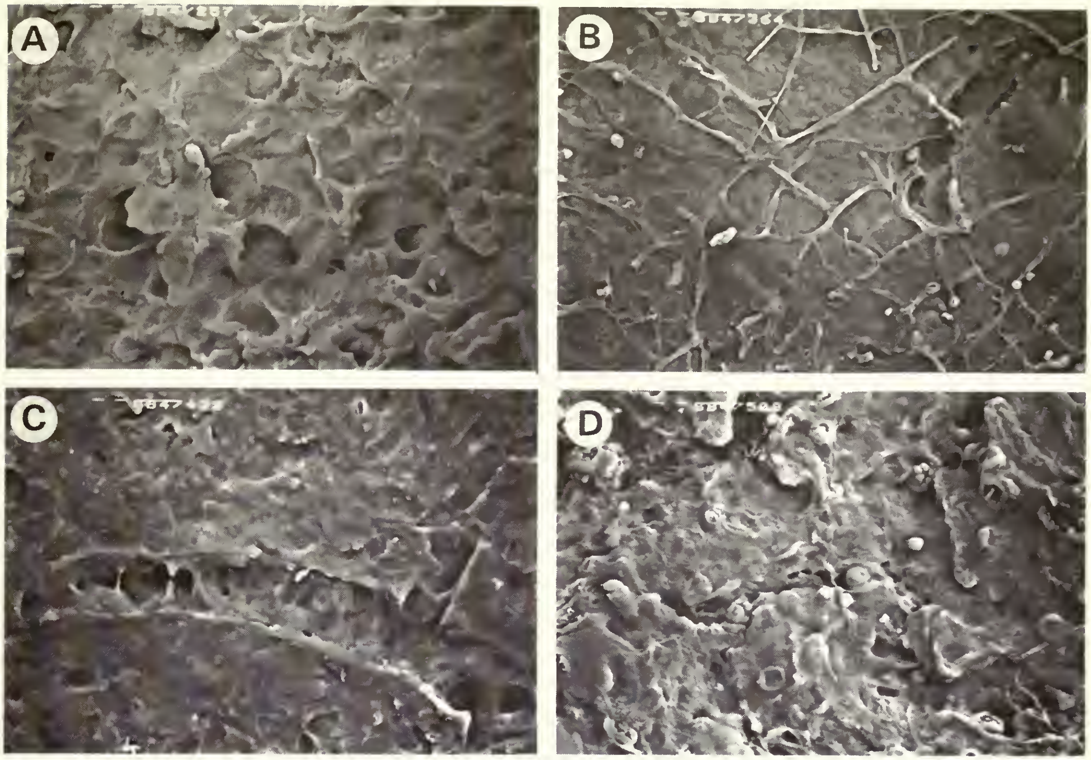


Fig. 11 Pored upper surface. A. *Pseudocyphellaria ardesiaca* × 1000. B. *P. chloroleuca* × 1000. C. *P. corbettii* × 1000. D. *P. fimbriata* × 1000.

appear as a black layer, even in the oldest herbarium specimens and seem never to be decolourized on long storage. Twenty-eight species of *Pseudocyphellaria* in New Zealand have a green photobiont and 20 species have *Nostoc* cyanobionts.

Cephalodia: Cephalodia occur internally in all taxa having a green primary photobiont and may be visible as ± hemispherical swellings of the upper or, more commonly, the lower surface. In all cases the secondary photobiont is *Nostoc* which produces heterocysts capable of fixing atmospheric nitrogen (Green *et al.*, 1980). Cephalodia develop in the medulla just below the photobiont layer (James & Henssen, 1976); a detailed investigation of the processes of cyanobiont capture and subsequent cephalodial development in New Zealand species of *Pseudocyphellaria* has not yet been made, although data is available for some South American taxa (Renner, 1980). Cephalodia in *Pseudocyphellaria* are widely reported in earlier literature (Nylander, 1860*a*, 1860*b*, 1867, 1868*c*, 1877, 1888*b*; Lindsay, 1867; Forssell, 1883; Stirton, 1900; Hue, 1901). Renner (1982*a*, 1982*b*) developed a cryptophotometric method for localizing secondary metabolites (depsides, depsidones, dibenzofurans, etc.) in internal cephalodia (e.g. in *P. faveolata*), and found such metabolites only in the outer enclosing envelope, the inner fungal tissue of the cephalodium being without detectable amounts of secondary metabolites. Earlier, Jordan (1972) recorded differences in chemistry between the vegetative thallus and external cephalodia in *Lobaria amplissima*.

According to Renner (1982*b*) the absence of secondary metabolites from the central parts of internal cephalodia in the Peltigerineae may be the result of a locally different mycobiont metabolism, such a difference possibly being connected with an adaptation of the mycobiont towards uptake and transformation of reduced nitrogen compounds (e.g. ammonium ions) released by nitrogen-fixing heterocysts. Since the rate of nitrogen fixation in *Pseudocyphellaria* cephalodia is high (Green *et al.*, 1980), and carbon dioxide assimilation is only of secondary importance in supplying carbon skeletons to the mycobiont, it seems likely that cephalodial mycobionts are ± exclusively supplied with reduced nitrogen compounds such as ammonia. Complete uptake of fixed nitrogen may be important in avoiding nitrogen-limiting conditions for its fixation, e.g. by a repression of enzyme synthesis in *Nostoc* heterocysts (Renner, 1982*b*).

The formation of cephalodia is analogous to the formation of photosymbiodemes (see below), except that in the latter case capture of a green photobiont by a cyanobiont-containing species results in the formation of the external photosymbiodeme.

Medulla: The medulla is composed of loosely to ± compactly interwoven, unorientated hyphae 2–5 μm diam. In some species (e.g. *P. crocata*, *P. faveolata*) ± moniliform hyphae are produced in the medulla (see Malme, 1899; Hue, 1901; Magnusson, 1940), such hyphae being similar to the knobbly hyphae seen in the medulla of species of *Leioderma* (Galloway & Jørgensen, 1987). In species with a yellow medulla, the hyphae are thickly encrusted with yellow crystals (see Green *et al.*, 1985:71, Fig. 7). The thickness of the medulla varies considerably between species, within individuals of the same species, and even within a single thallus, depending on the age and size of the thallus lobe, and on the particular microhabitat and microclimate conditions prevailing at a given part of the thallus.

Lower cortex: The lower cortex is a pseudoparenchymatous tissue very similar in structure to that of the upper cortex, although it is usually thinner than the upper cortex. Cells are colourless to yellow-brown or red-brown, with the outer-most cells being most strongly pigmented and the inner cell layers paler. The red-brown cortical pigment of *P. granulata* turns blue-green in K, a reaction not seen in any other species. Cells of the lower cortex are 2·5–15·5 μm diam., with walls 1·5–2·5 μm thick. The thickness of the lower cortex ranges from 9–60 μm, but within each species the variation observed within individual thalli is 4–14 μm.

Tomentum: Tomental hairs develop from the outermost cells of the lower cortex (Fig. 10) and also occasionally from those of the upper cortex (Fig. 1A, B). Hyphae are mainly simple, usually thick-walled, and with a prominent central canal, rarely 2–3-branched at apices or occasionally with short, lateral branchlets [analogous to structures seen on the tomental hairs of some species of *Sticta* (see Harris, 1984)], septate (often with constrictions at septa, and rarely ± moniliform), colourless, pale straw-yellow, yellow-brown to red-brown, solitary or more usually in conglutinate fascicles, 2–10(–20)-together, from 4·5–9 μm diam. and (30–)45–230(–450) μm long.

Ascomata: Ascomata in *Pseudocyphellaria* are hemiangiocarpic in development, arising from a compact primordium which develops in the lower part of the photobiont layer. The ontogeny of ascomata in *Pseudocyphellaria* is similar to that seen in *Lobaria* (Letrouit-Galinou, 1971) and is discussed in detail in Keuck (1977) and Henssen (1981). An important, and also the earliest, account of ascomatal development in *Pseudocyphellaria* (in *P. anthraspis*) is given by Sturgis (1890).

Exciple: The exciple refers to the whole supporting structure of thecial tissues in ascomata and may or may not contain photobiont cells. Species with a proper exciple (*excipulum proprium*), lacking photobiont cells have sessile apothecia and include *P. billardierei*, *P. carpoloma*, *P. chloroleuca*, *P. cinnamomea*, *P. coriacea*, *P. crassa*, *P. crocata*, *P. degelii*, *P. dissimilis*, *P. episticta*, *P. faveolata*, *P. fimbriata*, *P. fimbriatoides*, *P. glabra*, *P. granulata*, *P. haywardiorum*, *P. homoeophylla*, *P. intricata*, *P. knightii*, *P. lindsayi*, *P. lividofusca*, *P. maculata*, *P. multifida*, *P. murrayi*, *P. neglecta*, *P. pickeringii*, *P. rufovirescens*, and *P. wilkinsii*. In these taxa the proper exciple is a colourless to pale straw-yellow to yellow-brown cellular tissue 35–140(–320) μm thick, composed of rows of anticlinally arranged, radiating, ± isodiametric, round to oblong to ± irregular cells, 4·5–13·5(–18) μm diam., with walls 1·5–4·5 μm thick, lumina round to irregular (1·5–)3–7(–9) μm diam. The outer parts of the proper exciple are often split into pyramidal or wedge-shaped masses (Fig. 9D) giving a characteristic scabrid-verrucose macroscopic appearance (× 10 lens). Occasionally colourless, simple, septate hairs develop from outer excipular cells at the base of the apothecia.

Species with a thalline exciple (*excipulum thallinum*) contain photobiont cells in the exciple, the arrangement of tissues being similar to that found in the vegetative thallus. In addition, apothecia with a thalline exciple are markedly stipitate. Species with stipitate fruits include *P. aurata*, *P. colensoi*, *P. coronata*, *P. durietzii*, *P. gretae*, *P. hookeri*, *P. montagnei*, *P. physciospora*, *P. poculifera*, *P. pubescens*, and *P. rubella*.

Hypothecium: The hypothecium is a compact zone of densely ramifying hyphae below the hamathecium, usually pigmented (pale straw-yellow, yellow-brown, orange-brown to red-brown), opaque, (30–)45–90(–145) μm thick, mostly K– but occasionally becoming blue-green in K (*P. fimbriata*, *P. fimbriatoides*, *P. pickeringii*).

Thecium: The thecium is colourless to pale straw-yellow or pale brownish, to dilute orange-brown, occasionally somewhat granular, I+ blue, 45–200 μm tall (most fertile species have a thecium height of 80–150 μm), measured from the upper edge of the hypothecium to the lower edge of the epithecium, at the centre of the thecium. The thecium is in most cases K– but in the lower part of *P. faveolata* and in *P. fimbriatoides* it stains greenish in K.

Hamathecium: The hamathecium is composed of numerous, markedly conglutinate paraphyses, separating in K, simple, straight, septate, 1·5–2·5 μm diam., swollen, ± capitate at apices (4·5–5 μm), sometimes moniliform, with 3–5 apical vacuolate cells visible.

Epithecium: The epithecium, (6·5–)10–15(–22·5) μm thick, consists of a pigmented, ± granular gel external to and including the tips of the paraphyses, varying in colour from greyish olivaceous to yellow-brown or red-brown. In a number of species a distinct colour change in the epithecium pigments is noted when sections are irrigated with K. The epithecium of *P. billardierei* turns dark greenish black, those of *P. dureitzii*, *P. faveolata*, *P. granulata*, *P. hookeri*, *P. montagnei*, deep violet-purple, and those of *P. episticta* and *P. lindsayi* rose-pink. The remaining taxa show either no change in epithecial pigments or else the epithecium slowly decolorizes. The colour change of epithecial pigments of fertile species of *Pseudocyphellaria* was earlier noted by Hue (1901), Magnusson (1940), Imshaug (1977), and Galloway (1986*a*). See also White & James (1985: 13–15).

Asci: Asci in *Pseudocyphellaria* are always shorter than paraphyses, clavate with a tapering foot, to ± cylindrical, bitunicate, I+ blue, with thickened apices and an apical ring staining in Lugol's iodine, dehiscence semifissitunicate, the ring everting (Keuck, 1977; Honegger, 1978; Hawksworth *et al.*, 1983), and producing eight ascospores, uniseriately or biseriately arranged in the ascus.

Ascospores: Ascospores in *Pseudocyphellaria* are ellipsoid to fusiform-ellipsoid, rarely acicular-fusiform, with broadly rounded or narrowly tapering apices. Immature spores are simple, while mature spores are at first 1-septate, possibly the normal or general condition of the mature spore as suggested by Lindsay (1869:495), and at length become 3-septate. Occasionally over-mature spores with five or seven septa are seen. A number of species have 1-septate spores with a conspicuously thickened septum traversed by a thin canal joining the two polar locules (the so-called physcioid spores). Such spores, first noted by Nylander (1860*b*) are found in *P. billardierei*, *P. carpoloma*, *P. durietzii*, and together with 3-septate spores in *P. crassa*, *P. crocata*, *P. faveolata*, *P. granulata*, *P. gretae*, *P. hookeri*, *P. maculata*, *P. montagnei*, *P. neglecta*, and *P. pubescens*. Although called polarilocular in some earlier accounts (e.g. in Galloway, 1985*b*) these spores with thickened septa are not at all similar to true polarilocular spores as found in *Caloplaca* for example, but are reminiscent of those of *Physcia* (see Moberg, 1977) as claimed by Nylander and later authors. In a few species (e.g. *P. degelii*, *P. pickeringii*) ascospores are colourless even at maturity; however, normal spore colour is olivaceous to yellow-brown or dark brown at maturity with quite often a range of colours seen in sections of thecium or even in a single ascus.

The importance of spores of *Pseudocyphellaria* in the statistical analyses of local populations of this genus is emphasised by Imshaug (1977).

Anamorphs: Adequate description of both morphology and anatomy of anamorphs (conidial states) of lichen-forming fungi is increasingly required in modern taxonomic revisions and for discussion of modern concepts and terminology followed in this account see Vobis (1980), Vobis & Hawksworth (1981), and Coppins (1983).

Anamorphs of *Pseudocyphellaria* were first described by Lindsay (1859: 191–205; 1869: 494–495) under the genera *Ricasolia*, *Sticta*, and *Stictina*. Lindsay's detailed observations on conidiomata (pycnidia), conidiogenous cells, and conidia were supported by excellent hand-coloured illustrations and are as pertinent today as they were over 100 years ago. He drew attention to the uniformity of what he called spermatia (conidia) and sterigmata (conidiophores) throughout each of these genera, a conclusion supported by Vainio (1890) for *Pseudocyphellaria*, and by Hue (1901) for *Sticta* sens. lat. (including taxa referable to *Lobaria*, *Pseudocyphellaria*, and *Sticta*).

Conidiomata: Conidiomata develop from primordia in the photobiont layer. They are pycnidial (cited as spermogones by Lindsay and some later authors), ± immersed in the thallus, globose to ovoid in shape, 0·1–0·5(–0·8) mm diam., often visible on both upper and lower surfaces as shallow, hemispherical swellings, but most generally indicated by a dark brown, red-brown or black ostiole, 0·05–0·1 mm diam., and which may be plane, slightly elevated, or punctate-depressed. The ostiole is usually surrounded by a narrow, white or colourless halo (× 10 lens). Mature conidiomata are filled with long, simple to occasionally branched conidiophores, (20)40–50(–70) μm long, comprising rows of intercalary conidiogenous cells. Conidiomata in *Pseudocyphellaria* are of the *Lobaria* type (Vobis & Hawksworth 1981: 252–253). They may be frequent to sparse, even on different parts of the same thallus, and appear to be most common at lobe margins, on thalline ridges of faveolate species or towards the apices of non-faveolate species, often arranged in lines at margins and on ridges or ± randomly scattered, to crowded-confluent. Quite often conidiomata erode and fall out of the thallus, leaving empty, gaping pits. Lindsay (1859: 191–192) first described this phenomenon 'With age it [the ostiole] expands, and when the nucleus or body of the spermogone falls out, as frequently happens, it may become saucer-shaped, with ragged, generally thickened and dark-coloured margins. In this state, the ostioles of old spermogones sometimes have the aspect of black rings or discs, as occasionally in *S. aurata*. However large or small the ostiole or external protuberance of the spermogone, its body is almost in all cases a large white kernel of a dense horny tissue, which becomes gelatinous and semipellucid in water. From its density, it can easily be enucleated with the point of a needle.' Conidiomata in *Pseudocyphellaria* appear to be most frequently developed in fertile species and are rare or absent in taxa having copious development of asexual propagules, e.g. *P. ardesiaca*, *P. argyracea*, *P. aurata*, *P. bartlettii*, *P. crocata*, *P. granulata*, *P. gretae*, *P. haywardiorum*, *P. intricata*, *P. neglecta*, and *P. nermula*.

Conidiogenous cells: The conidiogenous cells of *Pseudocyphellaria* (and also those of *Lobaria* and *Sticta*) are all very similar in morphology and size, a fact noted first by Lindsay (1859: pl. X; 1869: tab. 60) and by Hue (1901). Cells are colourless, ± cuboid to somewhat irregular, 2·5–5 μm diam. They are phialidic and type VII in the arrangement of Vobis & Hawksworth (1981: 257).

Conidia: These are very uniform throughout *Pseudocyphellaria*, both in New Zealand and in other parts of its range, and also in *Lobaria* and *Sticta*. Conidia are colourless, short, bacilliform to slightly dumbell-shaped (the two poles being only slightly swollen and usually more intensely birefringent than the remainder of the cell), (2–)3–5(–7) × 0·5–1 μm.

Photosymbiodemes

In *Pseudocyphellaria* (also in *Lobaria*, *Nephroma*, *Peltigera*, *Solorina*, and *Sticta*) distinctive yet obviously closely related pairs of taxa exist, the major apparent difference between them being in the nature of the photobiont present. Recently, in *Pseudocyphellaria* particularly, joined thalli comprising a single mycobiont with two different photobionts were recorded (James & Henssen, 1976; Renner & Galloway, 1982; Galloway, 1985*b*), the green photobiont- and the cyanobiont-containing demes being given separate names for their free-living representatives which are usually in this genus subtly distinct when growing independently. The term photosymbiodeme is used for such combined thalli in preference to phycosymbiodeme as originally proposed (Renner & Galloway, 1982), being a more neutral term and not carrying with it any specific reference to algae since blue-green algae are now increasingly accepted as cyanobacteria.

In New Zealand both free-living green photobiont- and cyanobiont-containing species may exist in similar habitats alongside examples of joined thalli; *P. allanii-P. coriacea*, *P. hookeri-P. durietzii*, *P. knightii-P. lividofusca*, *P. murrayi-P. rufovirescens*, *P. margaretiae-P. pubescens* are presently known (the cyanosymbiodeme preceding the chlorosymbiodeme) and there seems, on available evidence, to be no particular microclimatic factor promoting formation of photosymbiodemes, though this has not yet been closely studied in the field. Presently, joined thalli are known from moist, humid habitats in moderate shade, either close to sheltered streams, or in ± deep gorges, or in areas of wet forest on slopes often shrouded in mist or cloud. As both chloro- and cyanosymbiodemes appear to be capable of independent existence and have characters which permit their taxonomic separation, they are given independent species names. As James & Henssen (1976) point out, the *International Code of Botanical Nomenclature* makes no allowance for the existence of joined thalli differing only in the nature of the photobiont present.

Renner & Galloway (1982) have shown that the development of photosymbiodemes follows a uniform pattern in *Pseudocyphellaria*, and that chlorosymbiodemes are produced secondarily by the mycobiont of the cyanosymbiodeme. Whenever a chlorosymbiodeme is formed it is of secondary origin and is characterized by an heteromerous arrangement of tissues. A comparison between development of internal cephalodia (see above) and of chlorosymbiodeme formation shows certain parallels. Formation of cephalodia may be regarded as the secondary lichenisation of a cyanobacterium (*Nostoc*), whereas the formation of a chlorosymbiodeme involves capture of a green photobiont by a species having a cyanobiont as its primary photobiont.

Of the known photosymbiodemes in New Zealand, only two cyanosymbiodemes are known in the fertile state (*P. hookeri* and *P. murrayi*). In all the cases mentioned above, the chlorosymbiodemes and cyanosymbiodemes are mirror images of each other morphologically speaking, neither symbiodeme produces asexual propagules, nor is there any major chemical difference between chlorosymbiodeme and cyanosymbiodeme. Since photosymbiodemes are known only from forest or scrub vegetation in humid habitats, photosymbiodeme formation may be a mechanism which is evolving to allow mycobionts to exploit a wider range of macrohabitat and/or microclimate conditions (see also James & Henssen, 1976).

Lichenicolous fungi

On many New Zealand species of *Pseudocyphellaria* distinctive black or blackish brown spots, stains or apothecia-like galls are produced on the upper (rarely on the lower) surface, the result of attack by one or more genera of lichenicolous fungi (Hawksworth, 1982*b*). Such parasitic fungi were first recorded from Otago collections of *Pseudocyphellaria faveolata*, *P. granulata*, and *P. rubella* by Lindsay (1867: 448–453; 1869: 496) under the name *Celidium dubium*. Peculiar apothecia-like structures on what is now known as *Pseudocyphellaria glabra* led Fée (1824–1825), who first investigated this Southern Hemisphere lichen, to make it the type of a new genus, *Delisea* Fée. However, since *Delisea* was first described in 1819 by Lamouroux for a genus of red algae, Fée renamed his new lichen *Plectocarpon* (Fée, 1824–1825; 1828). Hawksworth & Galloway (1984) showed the lichenicolous fungus *Lichenomyces* Trevisan, to be a synonym of *Plectocarpon*, and that the fungus causing apothecia-like galls on *Pseudocyphellaria glabra* must be called *Plectocarpon pseudosticta*. It is likely that several unidentified species of *Plectocarpon* are associated with New Zealand species of *Pseudocyphellaria*, and these are presently under investigation. *Pseudocyphellaria* is a member of the Peltigerales, of which a number of genera (e.g. *Lobaria*, *Nephroma*, and especially *Peltigera*) are rich in lichenicolous fungi (Hawksworth, 1982*a*). A study of the lichenicolous fungi occurring in Southern Hemisphere species of *Pseudocyphellaria*, together with comparative chemical studies, should reveal something of the past and present relationships within the genus as it is at present represented in cool-temperate southern regions.

Chemistry

In lichens, primary metabolites such as lipids and carbohydrates are important to the lichen association both metabolically and structurally. Carbohydrates, for example, occur widely in lichens and probably constitute the major part of the dry weight of the thallus in most lichens. Lichen carbohydrates can be conveniently divided into the following major groups: (1) polysaccharides, (2) sugars and oligosaccharides, and (3) polyhydric alcohols (for a recent review of relevant literature see Elix *et al.*, 1984). Polyhydric alcohols (polyols) are implicated in the transfer of carbon skeletons (probably as their phosphorylated derivatives) from autotrophic to heterotrophic partners in a variety of symbiotic associations including the lichens (Smith, 1975, 1981; Hill, 1976). In species of *Pseudocyphellaria* in New Zealand, the polyols D-arabinitol and mannitol are the major water-soluble compounds present and often occur in considerable abundance (unpublished observations).

However it is the complex array of secondary metabolites produced by lichens which are of the greatest utility in chemosystematic studies. Chemotaxonomy has a wide application in contemporary lichenology (Hawksworth, 1976) and is especially useful in helping to separate taxa at the species level in *Pseudocyphellaria* (Wilkins & James, 1979; Galloway *et al.*, 1983*b*; Galloway, 1986*a*). Substances from all three major pathways of secondary metabolism in lichens are found in New Zealand species viz., the acetate-polymalonate pathway, the mevalonic acid pathway, and the shikimic acid pathway (see Culberson, 1969; 1970; Culberson & Culberson, 1970; Culberson *et al.*, 1977; Santesson, 1973; Huneck, 1974; Mosbach, 1974; Elix *et al.*, 1984; Huneck, 1984*b*).

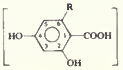
The richness and diversity of secondary metabolites found in species of *Pseudocyphellaria* (Wilkins & James, 1979; Galloway *et al.*, 1983*b*), and especially of the four series of triterpenoids discovered in New Zealand species (see below) has proved to be of great utility in the unravelling of species taxonomy. For instance, the very closely related faveolate species *P. billardierei*, *P. carpoloma*, *P. faveolata*, and *P. physciospora* all have a closely similar morphology and may often be difficult to distinguish on morphological grounds alone. However, they each have a distinctive chemistry and are readily separable chemically. Thus chemical characters reinforce differential morphological characters in closely related taxa and frequently allow the accurate determination of atypical material which otherwise might be difficult to differentiate on morphological grounds alone.

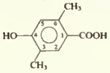
Within the family Lobariaceae there is a dramatic increase in the number and complexity of secondary metabolites as one moves from *Sticta*, through *Lobaria*, to *Pseudocyphellaria*. Species of *Sticta* have few or no secondary products soluble in acetone, instead they produce large quantities of water-soluble simple carbohydrates and methylamine; species of *Lobaria* have an intermediate range of secondary compounds, while species in *Pseudocyphellaria* have the most diverse secondary chemistry of the family, and one of the most complex chemistries of any lichen genus known. This chemical diversity is persuasive evidence for considering *Pseudocyphellaria* to be taxonomically remote from *Sticta* and more closely related to *Lobaria*. Indeed, there are probably good reasons for including *Sticta* in a family of its own (Stictaceae Zahlbr.) and keeping *Lobaria* and *Pseudocyphellaria* together in the family Lobariaceae Chev.

Compounds formed in each of the three pathways of secondary metabolism in *Pseudocyphellaria* are reviewed briefly below.

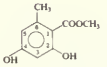
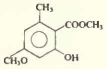
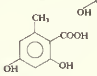
Acetate-polymalonate pathway

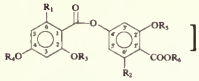
The most common phenolic acid units synthesized via the acetate-polymalonate pathway are of two kinds: (1) orcinol-type compounds based on the skeleton



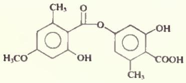
and β-orcinol-type compounds which have an extra C_1 substituent at the 3-position [] (Culberson, 1969).

A. *Orcinol series*

i) Monocyclic derivatives: methyl orsellinate [], 4-0-methyl-orsellinate [] and the parent orsellinic acid [] isolated from *Pseudocyphellaria crocata* by preparative two-way TLC (Maass, 1975*b*).

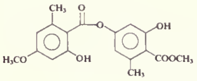
ii) *para*-depsides: The major structural variations seen in the orcinol *para*-depsides [] are the length of the polyketide derived side chains (R^1, R^2), the degree of oxidation of these side chains (CH_2COR or CH_2CH_2R), and the degree of methylation of the phenolic and carboxyl groups (R^3, R^4, R^5, R^6 = CH_3 or H) (Elix *et al.*, 1984).

1. *Evernic acid*



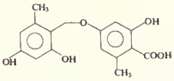
First isolated from *P. crocata* (Maass, 1975*b*)

2. *Methyl evernate*



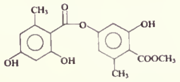
Isolated from *P. crocata* (Maass, 1975*b*) and from *Lobaria linita* (Maass, 1975*c*), and *Peltigera aphthosa* (Maass, 1975*a*).

3. *Lecanoric acid*



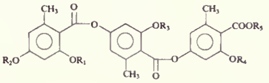
First isolated from *P. crocata* (Maass, 1975*b*)

4. *Methyl lecanorate*

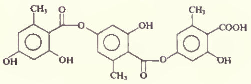


First isolated from *P. crocata* (Maass, 1975*b*).

iii) tridepsides: Besides variation in the degree of methylation of the phenolic and carboxyl groups (R^1, R^2, R^3, R^4, R^5 = H or CH_3), the orcinol tridepsides commonly have an additional OH (or OCH_3) group in the A-ring (Elix *et al.*, 1984).

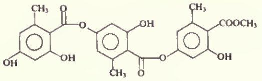


1. *Gyrophoric acid*



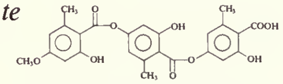
First isolated from *P. crocata* (Maass, 1975*b*) and from *P. sulphurea* (as *P. quercifolia*) by Maass (1975*d*).

2. *Methyl gyrophorate*



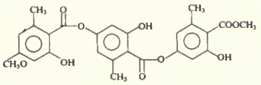
Isolated from *P. crocata*, *P. sulphurea*, and *Lobaria linita* by Maass (1975*b*, 1975*c*, 1975*d*).

3. *4-0-methyl gyrophorate*



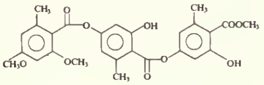
First isolated in *Pseudocyphellaria* from *P. crocata* and *P. sulphurea* (Maass, 1975*b*, 1975*d*).

4. *Tenuiorin*



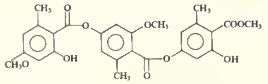
First isolated in *P. crocata* (Corbett & Cumming, 1971; Maass, 1975*b*).

5. *2-0-acetyltenuiorin*



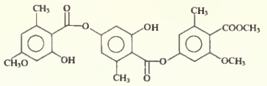
First isolated from *Pseudocyphellaria neglecta* by Bryan & Elix (1976). Also from *P. dissimilis*, *Peltigera dolichorhiza*, and *P. spuria*.

6. *2′-0-methyltenuiorin*



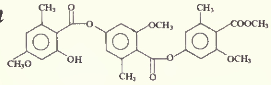
Isolated from *Pseudocyphellaria faveolata* (Elix & Lajide, 1981).

7. *2″-0-methyltenuiorin*



Isolated from *Pseudocyphellaria faveolata* (Elix & Lajide, 1981). Also in *P. billardierei* (Elix, 1986).

8. *2′,2″-Di-O-methyltenuiorin*

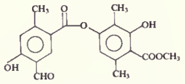


Isolated from *Pseudocyphellaria faveolata* (Elix & Lajide, 1981). Also in *P. billardierei* (Elix, 1986).

B. β-*Orcinol Series*

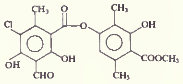
i) *para*-depsides

1. *Atranorin*



First isolated from *Pseudocyphellaria crocata* (Maass, 1975*b*).

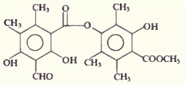
2. *Chloratranorin*



First isolated from *Pseudocyphellaria crocata* (Maass, 1975*a*).

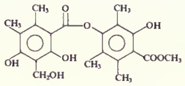
ii) Fully substituted depsides

1. *Pseudocyphellarin A*



Isolated from *Pseudocyphellaria endochrysa* (Huneck, 1984*a*; Huneck *et al.*, 1984). See also Elix & Lajide (1984).

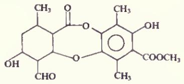
2. *Pseudocyphellarin B*



Isolated from *Pseudocyphellaria endochrysa* (see above).

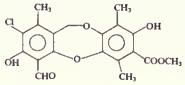
iii) Depsidones

1. *Methyl virensate (granulatin)*



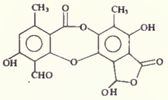
First isolated from *Pseudocyphellaria faveolata* and *P. granulata* (Renner *et al.*, 1978; Goh & Wilkins, 1979).

2. *Physciosporin (5-chloro methyl virensate, chlorogranulatin)*

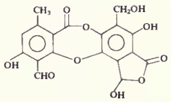


First isolated from *Pseudocyphellaria faveolata* and *P. granulata* (Renner *et al.*, 1978; Goh & Wilkins, 1979).

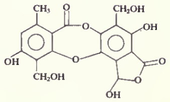
3. *Norstictic acid*



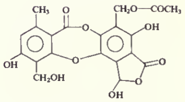
4. *Salazinic acid*



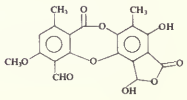
5. *Consalazinic acid*



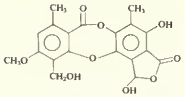
6. *Galbinic acid*



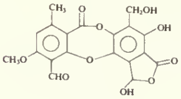
7. *Stictic acid*



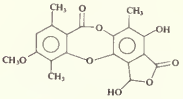
8. *Cryptostictic acid*


CH_3
O
CH_3
O
OH
CH_3O
O
CH_2OH
O
O
OH

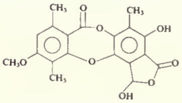
9. *Constictic acid*


CH_3
O
CH_2OH
O
OH
CH_3O
O
CHO
O
O
OH

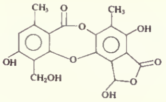
10. *Hypostictic acid*


CH_3
O
CH_3
O
OH
CH_3O
O
CH_3
O
O
HO

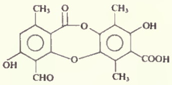
11. *Hyposalazinic acid*


CH_3
O
CH_3
O
OH
CH_3O
O
CH_3
O
O
OH

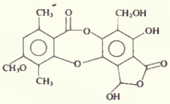
12. *Connorstictic acid*


CH_3
O
CH_3
O
OH
OH
O
CH_2OH
O
O
OH

13. *Virensic acid*

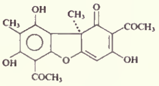

CH_3
O
CH_3
O
OH
OH
O
COOH
CHO
CH_3

14. *Hypoconstictic acid*


CH_3
O
CH_2OH
O
OH
CH_3O
O
CH_3
O
O
OH

A scheme showing the interrelationships of stictic acid and related depsidones is given in Elix *et al.* (1984: 194–195).

iv) *Usnic acid*

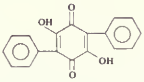

OH
CH_3
O
CH_3
$COCH_3$
OH
O
OH
$COCH_3$

Usnic acid occurs as a cortical pigment in *Pseudocyphellaria corbettii*, *P. freycinetii*, *P. glabra*, and *P. homoeophylla*.

Shikimic acid pathway

This pathway is responsible for the synthesis of terphenylquinones and pulvinic acid (4-Ylidenetetronic acid) derivatives. This biosynthetic route, accounting for a vast array of products in non lichen-forming fungi, leads to only a few of the compounds known in lichens (Culberson & Culberson, 1970). Terphenylquinones and 4-Ylidenetetronic acid derivatives are all pigments.

i) Terphenylquinones. Polyporic acid:

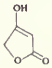


Zopf (1901, 1907) obtained from *Sticta orygmaea* (*Pseudocyphellaria coronata*) [collected by *Helms*, number 1214 in Arnold's exsiccata], a brown, sparingly soluble pigment 'orygmaeic acid', m.p.310°, which gave purple salts with alkalis. Zopf thought it might be an anthraquinone. Fifty years later, James Murray (1952) of the University of Otago (Dunedin, New Zealand), Chemistry Department, isolated orygmaeic acid from the New Zealand lichens *Pseudocyphellaria colensoi* and *P. coronata*, and showed that it was identical in structure to polyporic acid, discovered originally in the fungus *Polyporus nidulans*. Although able to distinguish chemically *P. coronata* and *P. colensoi*, Murray found some difficulty at first in separating these taxa solely on morphological criteria, and this led to his subsequent important taxonomic studies on New Zealand lichens. Sadly these were cut short by his tragically early death in 1961 at the age of 37. However, his initial chemical work formed the basis of three different and independent lines of study in New Zealand, Canada, and Germany.

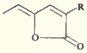
The antileukaemic activity of polyporic acid was discovered by Burton & Cain (1959). In the course of screening indigenous New Zealand plant products for experimental anti-cancer activity, a preparation of the lichen *P. coronata* was found to prolong significantly the lifespan of mice previously inoculated with an acute lymphocytic leukaemia. Polyporic acid isolated from the lichen was shown to possess antileukaemic activity and to account completely for that of the original crude extract.

The Rf's of polyporic acid isolated from *P. colensoi*, on t.l.c. in three solvent systems were recorded by Santesson (1967). Polyporic acid is known from *P. colensoi*, *P. coronata*, and *P. pickeringii* (Murray, 1952; Chin *et al.*, 1973).

ii) 4-Ylidenetetronic acids
Tetronic acid is a trivial name for 3-hydroxy-but-2-enolide.

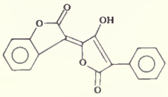


The corresponding 4-ylidene derivatives contain an additional exocyclic C-C double bond at C_4.



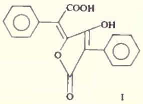
Natural products incorporating a 4-ylidenetetronic ring system have been known for almost a century, The ring system is a characteristic structural feature in the pulvinic acid group of yellow and red pigments found in lichens and known since 1879. These compounds also occur in the fungal families Boletaceae and Gomphidiaceae.

1. *Calycin*

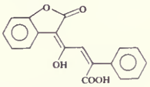


Its structure was accurately established by Åkermark (1961).

2. *Calycinic acid*



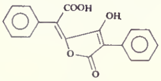
I



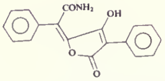
II

Isolated from *P. crocata* by Maass (1975 or *b*).

3. *Pulvinic acid*

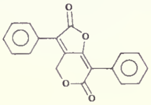


4. *Pulvinamide*



Isolated from *P. crocata* by Maass (1970*b*).

5. *Pulvinic dilactone*



The common pulvinic acid derivatives (pulvinic acid, pulvinic dilactone, and calycin) which nearly always occur together were first extracted from species of *Candelariella* and '*Lepraria*' in the late 19th century [for references to pre-1950 literature see Culberson (1969)]. These pulvinic acid derivatives are known from yellow-medulla species of *Pseudocyphellaria* particularly, and from those species having yellow pseudocyphellae (Murray, 1952; Maass *et al.*, 1964; Maass & Neish, 1967; Huneck & Follmann 1967*a*, 1967*b*; Maass, 1970*a*, 1970*b*; Corbett & Cumming, 1971; Chin *et al.*, 1973; Huneck *et al.*, 1973; Maass, 1975*b*; Wilkins & James, 1979; Galloway & James, 1980; Galloway *et al.*, 1983*b*; Galloway, 1985*b*, 1986*a*; Corbett *et al.*, 1987).

The yellow-medulla species of *Pseudocyphellaria* found most widely in New Zealand, *P. colensoi*, *P. coronata*, *P. pickeringii*, are commonly used as sources of dyes by spinners and weavers. The various yellow and orange pigments found in these lichens also attracted the interest of chemists in the late 19th century and Zopf (1892, 1899, 1901, 1907) isolated stictaurin, a 1:1 molecular complex of pulvinic dilactone and calycin, from a New Zealand specimen of what was then called *Sticta orygmaea* (*P. coronata*); he also obtained the compound from *P.*

aurata, *P. pickeringii* (as *Sticta flavicans*), *P. carpoloma* (his specimens of *Sticta glaucolurida* were from Arnold's Exsiccata 1199, the material being collected by Charles Knight), *P. crocata*, and *P. gilva*.

Biosynthesis of 4-Ylidenetetronic acids in *P. crocata* using C^{14}-labelled precursors was studied by Maass (Maass *et al.*, 1964; Maass & Neish, 1967; Maass 1970*a*, 1970*b*) [see also review of Pattenden (1978)], who showed that the basic pulvinic acid skeleton is derived via a phenylpropanoid precursor involving polyporic acid as a key intermediate.

Murray's work on *P. coronata* (Murray, 1952), also demonstrated distinctive red pigments easily extracted in organic solvents but proving unstable on purification. This pigment complex is not present in other related yellow-medulla species of *Pseudocyphellaria* and is therefore a useful screening test for *P. coronata.*

Mevalonic acid pathway

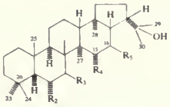
The mevalonic acid pathway produces sterols and triterpenoid skeletons, many of which occur in genera of the Peltigerineae. The exciting chapter of triterpenoid chemistry which has proved to be of such taxonomic usefulness in *Pseudocyphellaria* was anticipated by Murray (1952) who wrote 'Compound D has properties typical of a group of about 20 neutral unreactive substances which have been isolated from lichens . . . It is a colourless, highly crystalline substance, slightly soluble in most solvents, and optically active. It contains no methoxyl groups, shows no carbonyl or hydroxyl group reactions, and is unaffected by acid or alkali. Despite this lack of reactivity, the infra-red absorption spectrum has a strong carbonyl band at 1742 cm^{-1}. There is no absorption corresponding to hydroxyl groups. Although there is a weak absorption band in the UV below 220 mμ the substance appears to be saturated and the infra-red spectrum shows no ethylenic absorption. Compound D may be a triterpenoid, but owing to our inability to prepare any derivatives of it, we have not yet been able to define accurately its molecular formula.'

Murray's was the first in a series of chemical studies on New Zealand lichens, primarily species of *Pseudocyphellaria*, carried out by Corbett and his students at Otago University between 1966 and 1985, and by Wilkins and his collaborators at the University of Waikato. This work, one of the most productive and taxonomically important fields in New Zealand natural product chemistry, established the nature and identity of four series of triterpenoids based on hopane, stictane, fernene, and lupane skeletons, and has had profound consequences on taxonomic judgements in *Nephroma*, *Peltigera*, and especially in *Pseudocyphellaria* (Corbett & Young, 1966*a*, 1966*b*; Corbett & Smith, 1967; Corbett *et al.*, 1968; Corbett & Smith, 1969; Corbett & Cumming, 1971; Corbett & Heng, 1971; Corbett *et al.*, 1972; Chin *et al.*, 1973; Corbett & Wilkins, 1976; Corbett *et al.*, 1976; Corbett & Wilkins, 1977; Wilkins, 1977*a*, 1977*b*; Goh *et al.*, 1978; Ronaldson & Wilkins, 1978; Holland & Wilkins, 1979; Wilkins & James, 1979; Corbett *et al.*, 1982; Corbett *et al.*, 1985; Corbett *et al.*, 1987).

Terpenoids represent one of the largest and biologically most important classes of natural products, exhibiting a remarkable structural and functional diversity especially in view of their common origin from the same C_5 isopentenoid units. Although acetyl CoA is the basic building block of all terpenoids, mevalonic acid is the branch point separating terpenoid synthesis from other metabolic pathways. The term triterpenoid refers to a group of natural products containing 30 carbon atoms based on six isoprenoid units (Kulshreshtha *et al.*, 1972; Pant & Rastogi, 1979) produced from mevalonic acid and proceeding via the cyclisation of squalene from the intermediates geranyl pyrophosphate and farnesyl pyrophosphate in a scheme now universally accepted (Mabry & Gill, 1979). The polymerisation of six isopentenoid pyrophosphate units gives the 30C triterpenoid skeleton, and once the carbon-carbon bonds between the C_5 units are formed, they are remarkably stable. Subsequent to polymerisation and cyclisation with the formation of the triterpenoid skeleton, inumerable rearrangements, oxidations, etc. are possible, with the formation of thousands of structurally unique terpenoids possible.

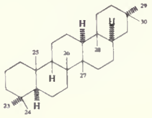
In *Pseudocyphellaria* four major triterpenoid series are known to date. Fernene triterpenoids were recently discovered in specimens of *Pseudocyphellaria aurata* (A. L. Wilkins, pers. comm.).

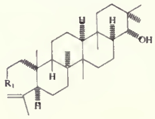
1. *Hopanes*



Corbett & Young, 1966*a*, 1966*b*; Corbett & Smith, 1967; Corbett *et al.*, 1968; Corbett & Smith, 1969; Corbett & Cumming, 1971; Corbett & Heng, 1971; Corbett *et al.*, 1972; Corbett & Wilkins, 1976, 1977; Ronaldson & Wilkins, 1978; Wilkins & James, 1979.

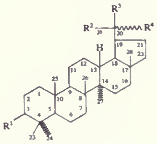
2. *Stictanes*





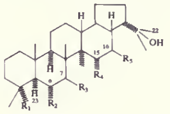
Chin *et al.*, 1973; Corbett *et al.*, 1976; Wilkins, 1977*a*, 1977*b*; Goh *et al.*, 1978; Holland & Wilkins, 1979; Corbett *et al.*, 1982.

3. *Lupanes*



Corbett *et al.*, 1985, 1987.

1. *Hopane series:* Hopanoid triterpenoids, which are thought to be 'primitive' phylogenetic precursors of sterols (Ourisson *et al.*, 1979), were first detected in species of *Pseudocyphellaria* by Corbett & Young (1966*a*, 1966*b*) who isolated and determined the structure of 7ß-acetoxy-22-hydroxyhopane (7β-acetoxyhopan-22-ol) (1) and 15α, 22-dihydroxyhopane (hopane-15α, 22-diol) (3) from *Sticta billardierii* [sic] (= *Pseudocyphellaria rufovirescens*). Since then, some 12 hopane triterpenoids have been detected in white-medulla species of *Pseudocyphellaria* (see above, and also Huneck & Follmann, 1967*a*, 1967*b*; Follmann & Huneck, 1972; Huneck *et al.*, 1973; Wilkins & James, 1979; Renner, 1980, 1982*b*; Renner & Galloway, 1982; Galloway *et al.*, 1983*b*; Huneck, 1984*b*; Galloway, 1986*b*). The recent report of these two hopanes in extracts of *Sphaerophorus scrobiculatus* (Huneck & Tibell, 1985) is presumed to be because of contamination with material of *Pseudocyphellaria* present in the collection.

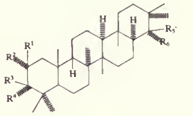


	R_1	R_2	R_3	R_4	R_5	
1	CH_3	H	OAc	H	H	7β-acetoxyhopan-22-ol (peltidactylin)
2	CH_3	H	OH	H	H	hopane-7β, 22-diol
3	CH_3	H	H	OH	H	hopane-15α, 22-diol
4	CH_3	OH	OH	H	H	hopane-6α, 7β, 22-triol
5	CH_3	OH	H	H	H	hopane-6α, 22-diol (zeorin)
6	CH_3	OAc	H	H	OAc	6α, 16β-diacetoxyhopan-22-ol
7	CH_3	OAc	H	H	OH	6α-acetoxyhopane-16β-22-diol
8	COOH	OAc	H	H	H	6α-axetoxy-22-hydroxyhopan-23-oic acid
9	COOH	OH	H	H	H	6α-22-dihydroxyhopan-23-oic acid
10	CH_3	OH	OAc	H	H	7β-acetoxyhopane-6α, 22-diol
11	CH_3	OAc	OH	H	H	6α-acetoxyhopan-7β, 22-diol
12	COOH	H	H	OAc		15α-acetoxy-22-hydroxyhopan-24-oic acid

Hopanes 5–11 (above) are often found in species of *Heterodermia*. The hopanes zeorin, pentadactylin, dolichorrhizin (15α-acetoxyhopan-22-ol), phlebic acid A (28-acetoxy-22-hydroxyhopan-23-oic acid), phlebic acid B(22-hydroxyhopan-23-oic acid), and hopane-

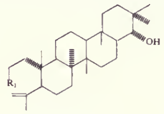
15α, 22-diol are known from Northern Hemisphere, and New Zealand species of *Peltigera* (Kurokawa *et al.*, 1966; Takahashi *et al.*, 1969, 1970; Tønsberg & Holtan-Hartwig, 1983; Galloway, 1985*b*; Vitikainen, 1985), and the hopanes zeorin, hopane-7β, 22-diol, 7β-acetoxyhopane-22-ol, hopane-15α, 22-diol, from species of *Nephroma* (Galloway, 1985*b*). Four hopane triterpenoids were isolated from *Physcia aipolia* by Elix *et al.* (1982) and were shown to be 20α-acetoxyhopane-6α, 22-diol, 16β-acetoxyhopane-6α, 22-diol, 6α-acetoxyhopane-16β, 22-diol, and 6α, 16β-diacetoxyhopan-22-ol.

2. *Stictane series:* A chair, boat, chair, chair, chair conformational sequence was proposed for stictane, the parent of 10 triterpenoids isolated by Chin *et al.* (1973) using column chromatography and multiple, preparative t.l.c. from the neutral fraction of hexane extractives of yellow-medulla species of *Pseudocyphellaria* from New Zealand (*P. colensoi*, *P. coronata*, and *P. pickeringii*).



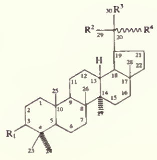
	R_1	R_2	R_3	R_4	R_5	R_6	
1	H	OH	OH	H	H	OH	stictane-2α, 3β, 22α-triol
2	H	OAc	OAc	H	H	OAc	2α, 3β, 22α-triacetoxystictane
3	H	OAc	OAc	H	H	OH	2α, 3β-diacetoxystictan-22α-ol
4	H	OH	OH	H	H	OH	2α-acetoxystictane-3β, 22α-diol
5	H	OAc	OAc	H	H	OH	3β-acetoxystictane-2α, 22α-diol
6	H	OAc	OAc	H	O		2α, 3β-diacetoxystictan-22-one
7	H	H	OH	H	H	OH	stictane-3β, 22α-diol
8	H	H	OAc	H	H	OAc	3β, 22α-diacetoxystictane
9	H	H	OAc	H	H	OH	3β-acetoxystictan-22α-ol
10	H	H	O		H	OH	22α-hydroxystictane-3-one
11	H	H	H	H	H	H	stictane

Three new *seco*-stictane triterpenoids were isolated from the New Zealand species *P. degelii* by Goh *et al.* (1978), possessing the novel 3,22-disubstituted 3,4-secostict-4(23)-ene structure

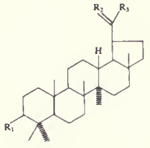


	R_1	
1	COOH	22α-hydroxy-3,4,-secostict-4(23)-ene-3-oic acid
2	CHO	22α-hydroxy-3,4,-secostict-4(23)-en-3-ol
3	CH_2OAc	3-acetoxy-3,4,-secostict-4(23)-en-22α-ol

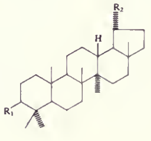
3. *Lupane series:* Twenty lupane triterpenoids including five (20RS)-epimeric pairs have been isolated and identified in the chloroform extractives of the yellow-medulla species *Pseudocyphellaria rubella* (Corbett *et al.*, 1985; 1987). All fractions obtained were complex mixtures, and multiple preparative layer chromatography (× 3) led to isolation of pure compounds. The following lupane triterpenoids were characterized:



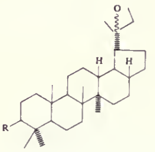
R_1	R_2	R_3	R_4	
OAc	CHO	CH_3	H	3β-acetoxylupan-29-al
OAc	CH_3	CH_3	OH	3β-acetoxylupan-20-ol
OH	CHO	CH_3	H	(20RS)-3β-hydroxylupan-29-al
OH	COOH	CH_3	H	(20RS)-3β-hydroxylupan-29-oic acid
OAc	COOH	CH_3	H	(20RS)-3β-acetoxylupan-20-oic acid
OH	CH_3	CH_3	OH	lupan-3β, 20-diol
OH	CH_2OH	CH_3	H	(20RS)-lupan-3β, 29-diol
OH	CH_3	H	OH	(20RS)-30-norlupane-3β, 20-diol
OH	CH_2OH	CH_3	OH	(20RS)-lupane-3β, 20, 29-triol
OAC	CH_2OH	CH_3	OH	(20RS)-3β-acetoxylupane-20, 29-diol



R_1	R_2	R_3	
OAc	CH_2	CH_3	3β-acetoxylup-20(29)-ene
OAc	O	CH_3	3β-acetoxy-30-norlupan-20-one
OAc	CH_2	CH_2OH	3β-acetoxylup-20(29)-en-30-ol
OH	O	CH_3	3β-hydroxy-30-norlupan-20-one
OH	CH_2	CH_3	3β-hydroxylup-20(29)-ene (lupeol)
OH	CH_2	CH_2OH	Lup-20(29)-en-3β, 30-diol



R_1	R_2	
OH	OH	20,29·30-trinorlupane-3β, 19α-diol
OAc	OAc	3β, 19α-diacetoxy-20,29,30-trinorlupane



R	
OAC	3β-acetoxylupan-20(29)-epoxide
OH	3β-hydroxylupan-20(29)-epoxide

Role of secondary metabolites in Pseudocyphellaria

Secondary metabolites are defined as those compounds having no recognized role in the maintenance of fundamental life processes in the organisms synthesizing them (Bell, 1981), a definition which excludes intermediate and/or end products of primary metabolic pathways, and photosynthetic pigments. The synthesis of secondary metabolites is complex, requiring multi-step reactions in a sequential pathway mediated by precisely regulated enzymes or multi-enzyme complexes (Luckner, 1980). Although there is conjecture over the adaptive significance of secondary plant metabolites (Siegler, 1981) there is now a large body of evidence supporting a primarily ecological role for these compounds, a proposition discussed particularly for lichens by

Rundel (1978). Secondary metabolites are implicated in a variety of ecological roles, as defensive agents for plants in plant-plant (allelopathic), plant-pathogen, and plant-herbivore interactions (Rhoades, 1979; Bell, 1980, 1981; Beart *et al.*, 1985).

In Southern Hemisphere, cool-temperate, rain-forests a diverse and luxuriant epiphytic lichen flora is well developed, with large, leafy species of *Pseudocyphellaria*, *Menegazzia*, *Nephroma*, and *Sticta* constituting a rich potential food supply for vertebrate or invertebrate herbivores. However, in Chilean *Nothofagus* forests Rundel (1978) records a surprising lack of predation on large, nutrient-rich lichens in the above mentioned genera, and suggests that the presence of terpenes may protect species producing them from herbivore predation. As with bryophytes, in New Zealand, Tasmania, and south-east Australia species of *Pseudocyphellaria* often reach a very great size (30–50 cm diam.) and normally show no evidence of attack by herbivores. It is possible that they are protected against herbivore predation by medullary and/or cortical secondary metabolites, such as pulvinic acid derivatives and triterpenoids. Thus, apart from their importance in species-level taxonomy, triterpenoids in *Pseudocyphellaria* may well prove to be effective anti-herbivore substances, an hypothesis ripe for experimental proof.

Green *et al.* (1985) suggest that in some species of *Pseudocyphellaria* both pulvinic acid derivatives and triterpenoids can provide a water-proofed CO_2 diffusion pathway from external pseudocyphellae, through the medulla to the photobiont layer, citing evidence from *P. colensoi* (p. 70, fig. 7).

Ecophysiology

Over the past 15 years there has been considerable progress made in the understanding of lichen ecophysiology, especially of water relations, gas exchange, photosynthetic rates, and respiratory rates (Rundel, 1982; Matthes & Feige, 1983; Kershaw, 1985; Lange & Ziegler, 1986). The main bulk of ecophysiological data on lichens comes from species present in relatively open habitats such as open woodland, tundra, deserts, and from the maritime Antarctic, with until recently, little data on lichens in dense forests, especially from rain-forest in cool-temperate and/or tropical areas (Green *et al.*, 1980).

A preliminary report on the physiological responses of *Pseudocyphellaria glabra* (and *Sticta stipitata*) in Tasmanian forest (Rundel *et al.*, 1979) was followed by a series of detailed ecophysiological studies [investigating CO_2 exchange, photosynthetic rate, respiratory rate, and water relations] on species of *Pseudocyphellaria* [*P. chloroleuca*, *P. colensoi*, *P. dissimilis*, *P. glabra*, *P. homoeophylla*, *P. hookeri*, *P. lividofusca*, *P. rufovirescens*] growing as conspicuous epiphytes in North Island *Nothofagus* forest (Green *et al.*, 1980, 1985; Snelgar *et al.*, 1980; Snelgar & Green, 1981*a*, 1981*b*; Brown *et al.*, 1981; Green & Snelgar, 1981; Snelgar, Green & Beltz, 1981; Snelgar, Green & Wilkins, 1981). These studies of Green and his colleagues conclusively demonstrate the suitability of species of *Pseudocyphellaria* for ecophysiological studies in rain-forest, and point to such dominant epiphytes as important components in the nutrient cycles of forest ecosystems.

Nitrogen fixation

The cyanobacterium *Nostoc* occurs widely in *Pseudocyphellaria*, both as a primary photobiont as well as in internal (rarely in external) cephalodia in species having green primary photobionts (James & Henssen, 1976). Cyanobacteria (blue-green algae) are microbial prokaryotes which show characters both of gram-negative bacteria and of eukaryotic algae. Those features of gram-negative bacteria are a prokaryotic cell structure with no membrane-bound organelles (e.g. chloroplasts), no distinct nucleus, 70S ribosomes, and a glycoprotein cell wall, while features characteristic of algae and higher plants include the capacity for oxygenic photosynthesis, possession of a non-cyclic photosynthetic electron-transport chain and presence of chlorophyll *a* (Stewart *et al.*, 1980). Nitrogen fixation in *Nostoc* and other cyanobacterial symbionts in lichens takes place in heterocysts, the frequency (20–25%) of heterocysts in cephalodia (Green *et al.*, 1980; Matthes & Feige, 1983) being higher than in vegetative tissue (5%) with a cyanobiont as primary photobiont. Cyanobacteria form associative symbioses

(Stewart *et al.*, 1979, 1985) with certain eukaryotic fungi, liverworts, ferns, gymnosperms, and angiosperms. Associations are uncommon or rare and have limited economic or ecological significance on a world basis, though nitrogen fixation by lichens is widespread in many ecosystems, and in several may be of considerable importance (Stewart *et al.*, 1979, 1980, 1985; Green *et al.*, 1980; Gibson & Jordan, 1983; Millbank, 1985*a*, 1985*b*; Sprent & Raven, 1985; Rowell *et al.*, 1985). Nitrogenous compounds (fixed from atmospheric nitrogen utilizing nitrogenase and other nitrogen-metabolising enzymes, such as glutamine synthetase and glutamate dehydrogenase), are lost from thalli of nitrogen-fixing lichens by leaching as a normal feature of their existence (Millbank, 1985*a*, 1985*b*). The loss of carbon compounds from lichens as a result of wetting after desiccation is now well documented (see Millbank, 1985*b*), and a similar situation exists with soluble nitrogen compounds (Crittenden, 1983) although the exact nature of the combined nitrogen lost from the thallus is not known.

In arctic tundra and taiga vegetation the nitrogen input into the ecosystem from lichen fixation is estimated at 0·5–1·5 kg hectare^{-1}, annum^{-1} (Alexander, 1981) which accounts for *c.* 50% of total nitrogen input, and in Colombian rain-forest, canopy lichens with cyanobionts contribute 1–8 kg hectare^{-1}, annum^{-1} to the forest ecosystem (Forman, 1975).

In a preliminary survey of 44 New Zealand lichens for nitrogenase activity (estimated by the acetylene-reduction technique), Green *et al.* (1980) surveyed 21 species of *Pseudocyphellaria*. Fixation rates were found to be species specific ranging from 0·2–32 nmol g^{-1}, min^{-1}. Rates of reduction were generally higher in species having a cyanobacterial symbiont (*P. crocata*, *P. dissimilis*, *P. hookeri*, *P. intricata*), although taxa with a green photobiont as primary symbiont also exhibited a range of reduction rates since all of these taxa have internal cephalodia containing *Nostoc*. Digestion of cephalodia with 10% chromium trioxide solution released filaments of cyanobiont with a frequency of heterocysts of 20–25%. The observed variation of nitrogen reduction rates in the different species of *Pseudocyphellaria* is not completely understood, but may be due to frequency of cephalodia in green photobiont species, and to climatic factors. Among species of *Pseudocyphellaria* with green photobionts, *P. homoeophylla* from sites in both North and South Is consistently reduced acetylene at low rates (2·1 nmols C_2H_2 g^{-1} min.$^{-1}$), *P. colensoi* consistently showed intermediate rates of reduction (4·6), and *P. rubella* consistently exhibited high rates of reduction (12·5). Higher reduction rates are found in species with high nitrogen contents. Nitrogen content is generally higher in *Sticta* (*S. fuliginosa*, *S. limbata*) than in *Pseudocyphellaria*, also in both genera cyanobiont-containing species have the higher reduction rates.

In *Pseudocyphellaria*, taxa with yellow medulla and pseudocyphellae tend to have lower reduction rates than species with white medulla and pseudocyphellae and in addition species with identical chemistry grouped together when acetylene reduction rates were plotted against nitrogen content (% dry wt). Thus taxa with a two-hopane chemistry had higher rates of reduction and higher nitrogen contents than taxa with two hopanes and stictic acid metabolites, and taxa with pulvinic acid derivatives. The results of Green *et al.* (1980), although still only preliminary, indicate that species of *Pseudocyphellaria* (and of *Sticta*) provide significant inputs of nitrogen into native forests in New Zealand, and are a good basis for further, more detailed work on the role of lichens in the nitrogen economy of rain-forest ecosytems. Species of *Pseudocyphellaria* 'are strongly represented in both species and quantity particularly in rain or cloud forests (above 700 m altitude) and must represent a large biomass. Environmental conditions are such, with heavy rainfall, and high insolation, that lichens could be metabolically active and fixing nitrogen for a considerable proportion of each year . . . Preliminary estimates of biomass indicate about 100 kg dry wt hectare^{-1} in the lowest two metres of beech forest of the Urewera National Park. This suggest a possible nitrogen contribution of between 1 and 10 kg N hectare^{-1} year^{-1} by the lichens, a significant input in these rain forests where the alternative nitrogen source would be rainfall averaging 1 to 2 kg N hectare^{-1} year^{-1}' (Green *et al.*, 1980: 348).

Snelgar & Green (1981*a*) found a positive linear relationship between rate of acetylene reduction and thallus water content. In a study of populations of the nitrogen-fixing species *P. dissimilis*, shade, mesic, and sun populations were compared. It was found that the upper cortex of all three populations were of equal thickness but that mesic and sun populations had a thicker photobiont layer and lower cortex, while the sun population had a thicker medulla and thicker and denser rhizines. These observed differences in thallus morphology correlated with evaporative demand of their environments. Sun (least shaded) populations are closely appressed to the substrate whereas shaded populations are only loosely attached and project from the substrate. Sun populations also show three adaptations which help maintain the lichen in a moist condition: (1) thalli have the classical xerophyte characteristic of reduced surface area to volume ratio (accounted for in the increase in thallus thickness); (2) an increased water storage capacity is attained by increased thallus thickness and a more developed rhizine layer; and (3) thalli are closely appressed to the substrate thereby assisting water storage by rhizines and reducing the area exposed to water loss by evaporation. Rates of acetylene reduction on an area basis (expressed as nmol $cm^{-2}min^{-1} \times 10^3$) for the three populations of *P. dissimilis* were: shade (164 ± 16), mesic (193 ± 10), and sun (262 ± 20), with the least shaded populations showing a decidedly increased rate of acetylene reduction as a result of the increased depth of cyanobiont layer.

Growth

New Zealand's forests [beech (*Nothofagus*) forest, beech-podocarp forest, and podocarp-mixed broadleaf (hardwood) forest] have a richly developed epiphytic lichen flora that is dominated by large, foliose species which form often visually striking clones (20–50 cm diam.), where conditions of light, humidity, and precipitation are optimal. Dominant epiphytes of tree trunks in such situations include: *Lobaria adscripta* (Galloway, 1981*b*), *Parmelia tenuirima* (Galloway & Elix, 1983), *Sticta subcaperata*, *S. latifrons*, and several species of *Pseudocyphellaria*, the most common being *P. billardierei*, *P. colensoi*, *P. coriacea*, *P. coronata*, *P. dissimilis*, *P. faveolata*, *P. fimbriata*, *P. glabra*, *P. gretae*, *P. homoeophylla*, *P. lividofusca*, and *P. rufovirescens*. Rundel (1980) speculates that the diversity and biomass of corticolous lichen communities in southern Chile, Tasmania, and New Zealand probably exceed those of corticolous communities anywhere in the Northern Hemisphere, and that the cool, humid conditions found in forested areas in these southern regions provide near ideal growing conditions for lichens. For a recent review of lichen growth and productivity see Matthes & Feige (1983).

The forested areas of New Zealand have a climate favourable for optimal lichen growth, rainfall being high [*c*. 150–300(–400) cm annually], and mist or cloud cover common throughout the year. Large foliose lichens are best developed on tree trunks (from below the canopy branches to near the ground) where there is a low evaporative stress as the ± closed canopy is 10–25 m above the ground. In closed forest, light is a limiting factor and only those species of *Pseudocyphellaria* with a cyanobiont as primary photosynthetic symbiont (usually *P. dissimilis* and *P. fimbriatoides* or locally *P. cinnamomea* and *P. hookeri*) are able to compete successfully with the bryophyte cover. The most spectacular growth of *Pseudocyphellaria* is to be found in the *Nothofagus* forests close to the Main Divide in South Island where *P. homoeophylla* is especially prolific, covering tree trunks up to 6 m above the ground and spreading over the forest floor in large swards. As a general rule, the richest development of epiphytic species occurs at forest margins, and near edges of lakes rivers, and streams where humidity is high and light is sufficient.

The large size and luxuriant habit of the species of *Pseudocyphellaria* mentioned above, as well as of various fruticose taxa (e.g. *Sphaerophorus*, *Thysanophoron*) implies high growth rates and this is confirmed in the relatively few measurements made to date (Snelgar & Green, 1982). Growth rates of several species of *Pseudocyphellaria* and of the fruticose *Sticta filix* were calculated from sequential photographs taken over a two-year period in *Nothofagus* forest in the Urewera National Park, North Island, New Zealand. Mean annual increases in *P. homoeophylla* and in *Sticta subcaperata* were linearly related to thallus diameter and ranged from 2·0–27·0 mm and 3·0–16·7 mm respectively. Growth rate estimates for 32 individual thalli were taken over periods of 386 to 733 days. Both taxa showed a dependence of growth rate on thallus size (not constant radial growth), a situation generally found only in small thalli (Topham, 1977). Other species examined had the following mean annual growth rates: *P. faveolata* (3·7–13·1 mm), *P. lividofusca* (4·6–9·4 mm), and *Sticta filix*, a fruticose, stalked species but ± lobate above the stalk (9·3–20·0 mm). Useful information on lichen biomass in Tasmanian rain forests is given in Kantvilas (1985).

Relatively rapid growth rates in New Zealand lichens are not only restricted to foliose and fruiticose species in forested areas. In high-alpine regions and on glacial moraines the growth rates of the crustose lichen *Rhizocarpon geographicum* have had some application in dating Holocene glacial deposits. The growth rate of this species in the Mt Cook area is one of the most rapid recorded anywhere in the world for this lichen, being 62·5 mm per 100 years (Burrows & Orwin, 1971; Birkeland, 1981). A high growth rate is to be expected for the Mt Cook area because of the high annual precipitation there (over 4 m per year).

The high growth rate of many epiphytic species of *Pseudocyphellaria* in New Zealand, together with their production of medullary triterpenoids which inhibit predation by herbivores, make these plants an important component of the forest biomass. Green *et al.* (1980) have published a preliminary estimate of the biomass of epiphytic lichens in the lowest two metres of the beech forest of Urewera National Park amounting to 100 Kg dry weight per hectare.

Geographical setting

New Zealand is an island archipelago and has been so throughout the greater part of its geological history (Fleming, 1979*a*). It consists of three main islands (North, South, and Stewart) and numerous smaller islands or island groups (Antipodes, Auckland, Bounty, Campbell, Chatham, Kermadec, Snares, and Three Kings), extending over *c.* 23° of latitude or some 2500 Km, in the South Pacific Ocean, from the subtropical Kermadec Islands in the north, to the subantarctic Campbell Island in the south. The New Zealand landmass is surrounded by a shallow, well-defined submarine platform, the continental shelf, sloping gently downwards from the intertidal zone to 150–180 m. Below this level, the seafloor gradient steepens abruptly and passes into the continental slope which plunges to depths usually greater than 1000 m.

The islands of New Zealand lie at the hub of a complex of submarine plateaux and ridges with intervening basins and associated deep trenches (Fig. 12). To the south-east and north-west of New Zealand, the Campbell Plateau (Adams, 1983; Adams *et al.*, 1979), Chatham Rise, Lord Howe Rise, Norfolk Ridge are presumed remnants of the former continental margin and peripheral geosynclinal belt of the Pacific (Panthalassic) margin of Gondwanaland. The submarine ridges and plateaus represent crustal strips separated from each other, and from Australia and Antarctica by rifting, with formation of new sea floor below the Tasman Sea, and the south-western Pacific Ocean continuing since late Cretaceous times. In contrast, the Kermadec-Colville ridge system to the north, north-east, and the Macquarie Ridge to the south-west of New Zealand, are seismically active, volcanic island arcs formed concurrently with new sea floor during the Cenozoic (Cullen, 1976, 1978).

New Zealand lies at the boundary of the India-Australian Plate and the Pacific Plate; the deep Kermadec (north-east) and Puysegur (south-west) trenches denote subduction zones, where the edge of one crustal plate is forced under its neighbour. In the north-east, Pacific Ocean floor is being subducted under the edge of the India-Australian Plate, while to the south-west, the Pacific Plate is being pushed over the India-Australian Plate. The Alpine Fault, a transcurrent fault of considerable tectonic activity, links these two subduction zones (Stevens, 1980*b*).

Ecology

Habitats

Habitats available to lichens in New Zealand are particularly various over a limited area, a consequence of diverse geology, vegetation, and climate. Conditions range from subtropical to alpine within relatively short distances, precipitation varies from 350 to 12,000 mm per annum, and the three main islands cover 13° of latitude, comprising between them a widely varying topography from rocky shore to glaciated summit. The lichen flora of New Zealand is extremely

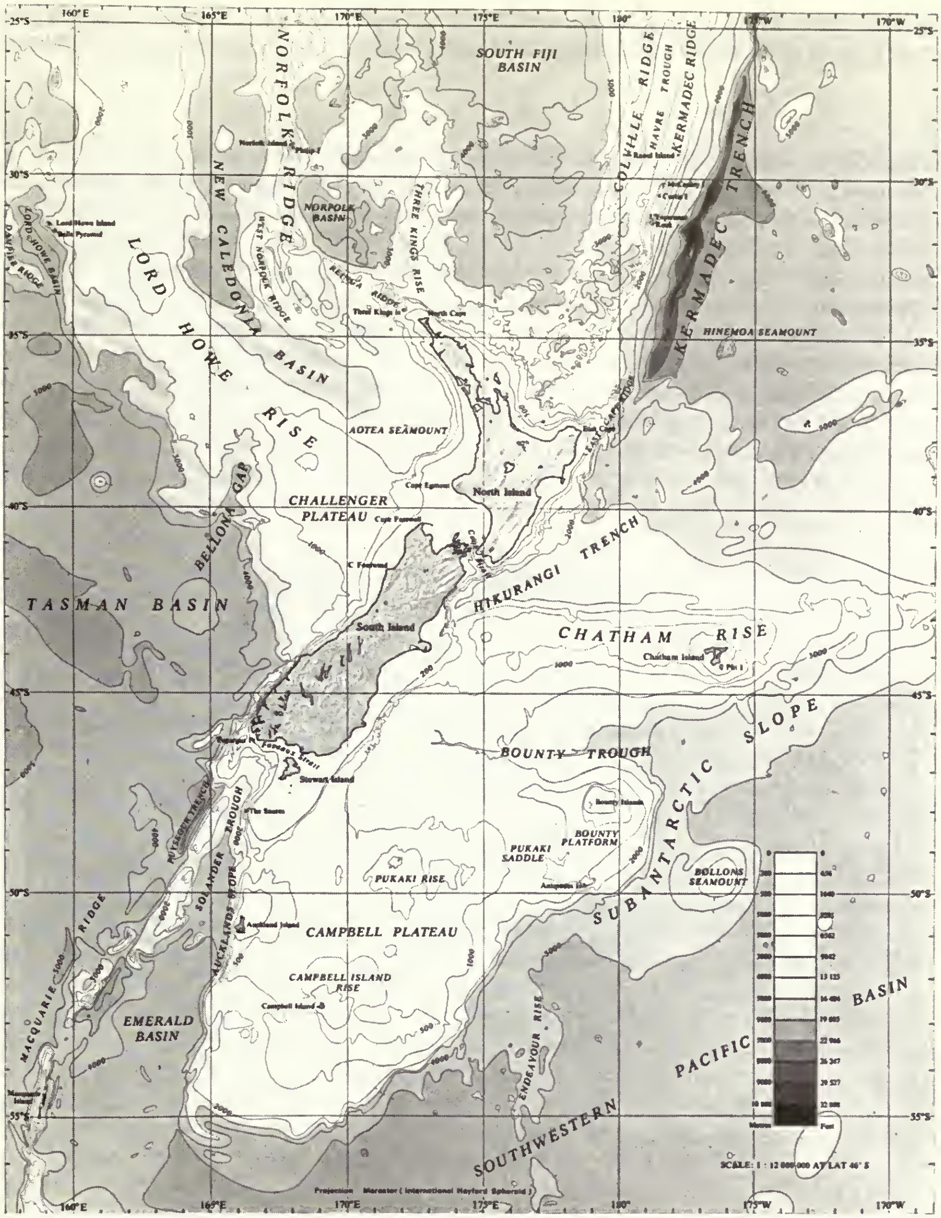

SOUTH FIJI BASIN
NORFOLK RIDGE
COLVILLE RIDGE
HAVRE TROUGH
KERMADEC RIDGE
KERMADEC TRENCH
NEW CALEDONIA BASIN
NORFOLK BASIN
WEST NORFOLK RIDGE
THREE KINGS RISE
REINGA RIDGE
LORD HOWE RISE
LORD HOWE BASIN
DAMPIER RIDGE
HINEMOA SEAMOUNT
AOTEA SEAMOUNT
CHALLENGER PLATEAU
BELLONA GAP
North Island
South Island
HIKURANGI TRENCH
TASMAN BASIN
CHATHAM RISE
Chatham Island
BOUNTY TROUGH
SUBANTARCTIC SLOPE
Stewart Island
PUYSEGUR TRENCH
SOLANDER TROUGH
AUCKLANDS SLOPE
BOUNTY PLATFORM
PUKAKI SADDLE
PUKAKI RISE
BOLLONS SEAMOUNT
CAMPBELL PLATEAU
CAMPBELL ISLAND RISE
MACQUARIE RIDGE
EMERALD BASIN
ENDEAVOUR RISE
PACIFIC BASIN
SOUTHWESTERN
160°E
165°E
170°E
175°E
180°
175°W
170°W
25°S
30°S
35°S
40°S
45°S
50°S
55°S
SCALE 1 : 12 000 000 AT LAT 46° S

Fig. 12 New Zealand and the surrounding ocean floor showing submarine plateaux and ridges with intervening basins and deep trenches (Cullen, 1976).

diverse, reflecting this rich array of habitats, and comprises in excess of 200 genera (Galloway, 1985*b*).

Species of *Pseudocyphellaria* are primarily epiphytes in forest and scrub vegetation (see below), although a few species also grow on soil, viz., *P. dissimilis* in low-light environments on the forest floor or over rocks, in warm, moist, temperate rain-forest [especially in podocarp or podocarp-broadleaved, hardwood forest in south-eastern and western South Island, and throughout North Island]; *P. crocata*, *P. neglecta*, and *P. pickeringii* on stones or boulders (rarely on walls) in dry, sunny, open sites in short grassland; and *P. crocata* (occasional), *P. degelii*, *P. glabra*, *P. maculata*, and *P. pickeringii*, and occasionally *P. neglecta*, on soil or on rocks in subalpine tussock grassland dominated by species of *Celmisia* and *Chionochloa* (snowgrass), or at the base of subalpine scrub such as *Cassinia*, *Dracophyllum*, or *Olearia*.

Climate

New Zealand lies across the mid latitude zone of westerly winds, and its climate is greatly influenced by this predominant wind flow (Coulter, 1973; Tomlinson, 1976; Fleming 1979*b*). New Zealand occupies an isolated position in a vast domain of ocean (Fig. 13) which ensures that the westerly winds reaching it are moisture-laden; hence in many parts and especially on western coasts and in mountainous regions, humid conditions are common. The passage of winds over great expanses of ocean has a moderating effect on the air temperature. The main mountain ranges of New Zealand are aligned north-east/south-west, and offer a major barrier to the prevailing moisture-laden westerlies, and in South Island especially, western slopes of the Main Divide receive very high rainfalls (to 12,000 mm per annum). East of the Main Divide, rainfall drops progressively in a rapid gradient, with the intermontane basins of Central Otago and Canterbury receiving the lowest rainfalls of any region in the country (to 350 mm per annum).

Species of *Pseudocyphellaria* are found in New Zealand in five bioclimatic zones viz., subtropical, warm temperate, cool temperate, subantarctic, and low antarctic (nomenclature

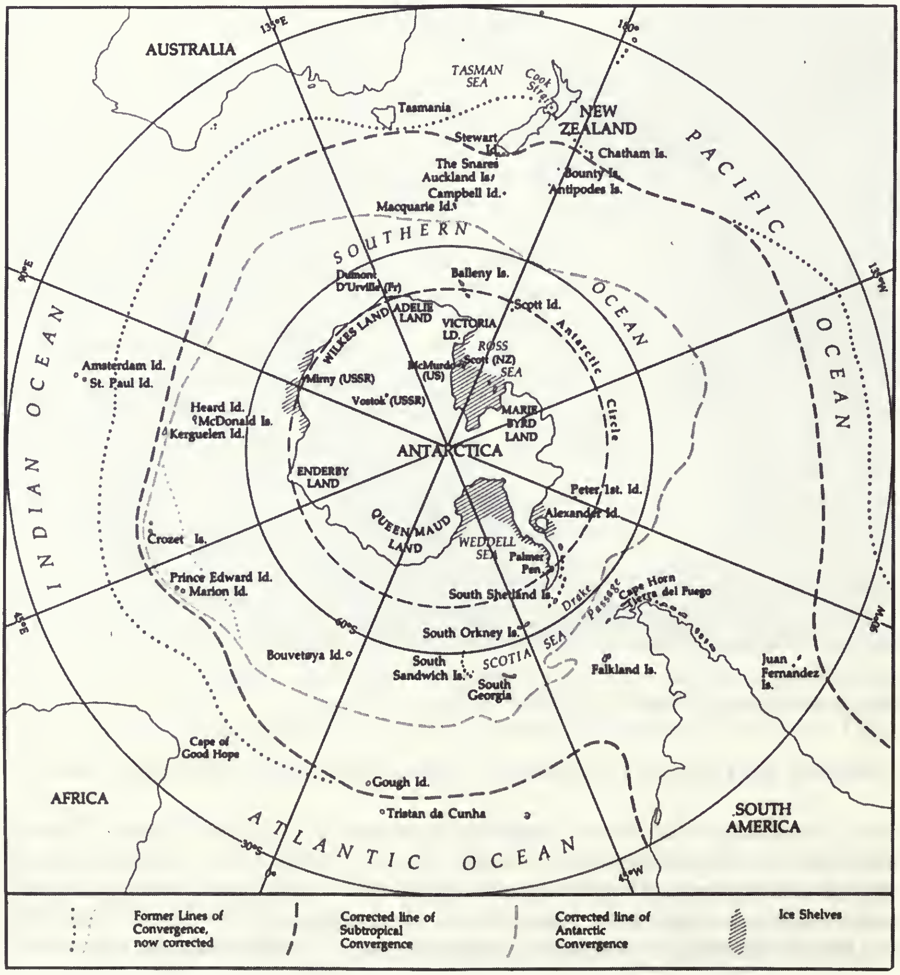

AUSTRALIA
135°E
180°
TASMAN SEA
Cook Strait
Tasmania
NEW ZEALAND
Stewart Id.
Chatham Is.
The Snares
Auckland Is.
Campbell Id.
Bounty Is.
Antipodes Is.
Macquarie Id.
PACIFIC
SOUTHERN OCEAN
135°W
90°E
Balleny Is.
Dumont D'Urville (Fr)
ADELIE LAND
Scott Id.
VICTORIA LD.
WILKES LAND
ROSS SEA
Scott (NZ)
McMurdo (US)
Antarctic Circle
Mirny (USSR)
Vostok (USSR)
MARIE BYRD LAND
ANTARCTICA
Amsterdam Id.
St. Paul Id.
Heard Id.
McDonald Is.
Kerguelen Id.
INDIAN OCEAN
OCEAN
ENDERBY LAND
Peter 1st. Id.
Alexander Id.
QUEEN MAUD LAND
WEDDELL SEA
Palmer Pen.
Crozet Is.
Prince Edward Id.
Marion Id.
South Shetland Is.
Drake Passage
Cape Horn
Tierra del Fuego
45°E
60°S
90°W
South Orkney Is.
SCOTIA SEA
Bouvetøya Id.
South Sandwich Is.
South Georgia
Falkland Is.
Juan Fernandez Is.
Cape of Good Hope
Gough Id.
AFRICA
Tristan da Cunha
SOUTH AMERICA
ATLANTIC OCEAN
30°S
0°
45°W
Former Lines of Convergence, now corrected
Corrected line of Subtropical Convergence
Corrected line of Antarctic Convergence
Ice Shelves

Fig. 13 New Zealand and the southern oceans and landmasses.

follows Meurk, 1984) with most taxa represented in warm-temperate and cool-temperate zones between lats 35°S and 48°S.

Vegetation

New Zealand's native vegetation derives from plants which have survived from Gondwanan times when New Zealand was part of the Panthalassic margin of that great southern landmass, as well as from those which arrived by long-distance dispersal during some 60 million years of isolation. The New Zealand flora comprises *c.* 2000 species of vascular plants of which about 40 genera and 85% of the species are endemic. This high degree of endemism at species and generic levels (there are no endemic families), and the noteworthy development of certain genera such as *Hebe*, is sufficient to give New Zealand the status of a distinct botanical region (Good, 1974; Godley, 1976). The vegetation is extremely varied since habitat conditions range from subtropical to alpine, precipitation is from 350 to 12,000 mm per annum, and there is a great diversity of sites. Species of *Pseudocyphellaria* are found mainly in two principal vegetation types, forest communities from sea-level to tree-line and in subalpine-alpine scrub and/or grassland communities above tree-line.

Forest: It is generally accepted that at the advent of Polynesian settlement, *c.* 1000 years ago, some 75% of the total land surface had a continuous forest cover, amounting to *c.* 20,000,000 hectares. Forest was absent from the 15% of the country lying within the alpine zone, and from a further 2% of mostly lowland swamps or bogs, gravel floodplains, and coastal sand dunes. The remaining 8% of New Zealand comprises areas of very low rainfall, <650 mm per annum, and in these areas was probably a mosaic of forest, scrub, and tussock-grassland, subject to occasional lightning fires, but not true savannah. These irregularly forested districts were mainly in the eastern parts of South I., but were locally significant also in parts of North I. (Nicholls, 1980). As a result of Polynesian and natural fires (McGlone, 1983), and later logging and land clearance subsequent to European settlement from 1840 to the present, natural forests cover *c.* 23% of the land surface (a little over 6,000,000 hectares), mainly in upland or mountainous areas often with high rainfall.

Main canopy species of New Zealand forests are generally characterized as 'softwoods' (coniferous species) or 'hardwoods' (dicotyledonous species), and four main physiognomic elements are recognized viz., kauri (*Agathis australis*) forest; beech (*Nothofagus*) forest; softwood forest; and broadleaf hardwood (hardwoods other than beech) forest (Robbins, 1962; Dansereau, 1964; Poole & Adams, 1980; J. Wardle, 1984).

46% of New Zealand's indigenous forests are 'pure beech forest' with a canopy dominated by species of *Nothofagus*, and 22% of the forests are mixtures of beech with conifers or broadleaf hardwoods (J. Wardle, 1984). Of the beech species, silver beech (*Nothofagus menziesii*) is most common when the climate is cool and wet, and large silver beech forests are found in montane and subalpine areas of the western parts of South I. Mountain beech (*N. solandri* var. *cliffortioides*) occurs in montane and subalpine zones of drier areas and forms extensive natural monocultures in the central parts of South I. Red beech (*N. fusca*) is primarily confined to lowland or montane forests occupying deep, fertile soils. Black beech (*N. solandri* var. *solandri*) and hard beech (*N. truncata*) usually occur at lower altitudes in forests mixed with conifers and/ or with other hardwood species.

The remaining 32% of New Zealand's indigenous forests are dominated by conifers and hardwoods other than *Nothofagus*. Kauri forest occurs in the northern parts of North I., with *Agathis australis* emerging from a canopy of other conifers such as *Phyllocladus trichomanoides*, and hardwoods e.g., *Beilschmiedia tawa*, *Knightia excelsa*, *Weinmannia silvicola*, and other trees.

Forests dominated by other softwoods (mainly podocarps such as *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, etc.) are found mainly on moderately fertile soils in North I. (e.g. in Urewera National Park), and at low altitudes (e.g. in Westland).

Conifer-broadleaf hardwood forest with a mixed canopy of conifers and hardwoods other than beeches, are found mainly in steepland areas with wet climates.

Conifer-broadleaf hardwood forests occur especially in montane areas with a mild climate and relatively high rainfall. They are especially well-developed in central Westland. The steepland montane conifer-broadleaf hardwood forests are commonly characterized by few dominant canopy species, mainly *Metrosideros umbellata*, *Weinmannia racemosa*, and *Quintinia acutifolia*. At lower altitudes (600 m) these angiosperms are associated with the conifers *Dacrydium cupressinum* and *Prumnopitys ferruginea*, and at higher altitudes (800 m), *Libocedrus bidwillii* and *Podocarpus hallii*.

In beech forests and in mixed beech-podocarp forests especially, species of *Pseudocyphellaria* reach their maximum diversity, development, and abundance, sometimes as ground cover (*P. homoeophylla*), but more commonly as epiphytes, with extensive clones of the following species often present: *P. colensoi*, *P. coronata*, *P. degelii*, *P. faveolata*, *P. homoeophylla*, *P. multifida* and *P. rufovirescens*.

At altitudes above *c.* 1000 m, forest gives way to alpine vegetation (see below), with or without a zone of scrub at tree-line separating the forest from the tussock-grasslands and fellfield of the alpine zone. Tree-line, a major ecological boundary (see P. Wardle, 1985) represents the altitude at which climate becomes too cold to support growth of trees. In New Zealand two species of *Nothofagus* form most tree-lines; on drier mountains *N. solandri* var. *cliffortioides* grows as pure stands, and on wetter mountains both this species and *N. menziesii* occur together with a much richer accompanying flora. On the latter species at tree-line, a rich selection of *Pseudocyphellaria* is met with, including *P. ardesiaca*, *P. corbettii*, *P. episticta*, *P. glabra*, *P. granulata*, *P. gretae*, *P. lividofusca*, *P. pickeringii*, *P. pubescens*, and *P. rubella*.

However, *Nothofagus* is widely absent in areas deforested during Pleistocene glaciation, or volcanism (P. Wardle, 1964; J. Wardle, 1984), and instead there are floristically complex treelines of small trees and large shrubs belonging to genera such as *Podocarpus*, *Dacrydium* (Podocarpaceae), *Hoheria* (Malvaceae), *Senecio* and *Olearia* (Compositae), *Dracophyllum* and *Archeria* (Epacridaceae), and *Hebe* (Scrophulariaceae). Species of these genera often form a dense, interlocking subalpine scrub zone which can extend for 100–300 m above the upper limit of tall forest. Species of *Pseudocyphellaria* found in subalpine scrub include *P. crocata*, *P. degelii*, *P. faveolata*, *P. glabra*, and *P. maculata*..

Alpine vegetation: The alpine zone in New Zealand (of some 1000 m elevation) extends from the tree-line, where present, upwards to the summer snowline, the level to which snow thaws during most summers (Mark, 1979). Above tree-line there is generally a belt of grassland dominated by several tall species of snow tussock (*Chionochloa*), sometimes also with an important co-dominant shrub component such as *Aciphylla* or *Dracophyllum*. This zone is termed the low-alpine zone (P. Wardle, 1964; Mark, 1979), and comprises mixed snow tussock scrub (Mark & Adams, 1973) including species of *Chionochloa* together with scrub species such as *Dracophyllum uniflorum*, *Hebe odora*, *Phyllocladus alpinus*, *Podocarpus nivalis*, etc., and also snow tussock herbfield with *Chionochloa* and species of *Aciphylla*, *Anisotome*, *Celmisia*, and occasionally *Dracophyllum* and *Hebe*. In snow tussock herbfield which Mark & Bliss (1970) regard as being the lower level of the high-alpine zone, the following species of *Pseudocyphellaria* are found: *P. degelii*, *P. glabra*, *P. maculata*, and *P. pickeringii*, either among tussocks or herbs such as *Celmisia viscosa*, or at the bases of low scrub (*Aciphylla* or *Dracophyllum*). In the high-alpine zone (P. Wardle, 1964; Mark & Bliss, 1970; Mark & Adams, 1973; Bliss & Mark, 1974; Mark, 1979; Gibson & Kirkpatrick, 1986) vegetation is low and less continuous and consists of fellfield, cushion vegetation, snowbank vegetation, and scree. The only species of *Pseudocyphellaria* which penetrate into the high-alpine zone are *P. degelii*, *P. glabra*, and *P. maculata*, some or all being found in fellfield on the Central Otago mountains (Mark & Bliss, 1970), and on mountain ranges of Canterbury from Mt Technical to the Kirkliston Range.

The tussock grasslands and tundras of the subantarctic shelf islands (Antipodes, Auckland, Campbell, and Macquarie Is) are closest ecologically to the snow tussock grasslands and high-alpine tundras of the central and eastern mountains of South I. (Bliss, 1979), and in these exposed subantarctic habitats, *P. degelii*, *P. glabra*, and occasionally *P. physciospora* occur. In contrast, the Low Subantarctic closed forest (*Metrosideros*) of the Auckland Is and the High

Subantarctic scrub (*Dracophyllum*) of the Auckland and Campbell Is (Bliss, 1979) supports a more diverse assemblage of *Pseudocyphellaria* including *P. billardierei*, *P. coronata*, *P. faveolata*, *P. glabra*, *P. multifida*, *P. physciospora*, and *P. rubella*.

Factors affecting distribution of Pseudocyphellaria

Detailed studies on the ecology and phytosociology of cool-temperate South Pacific lichens are still in their infancy, the most comprehensive account to date being that of Kantvilas (1985) on Tasmanian rain forest macrolichens. Apart from a preliminary phytosociological study of cryptogamic epiphytes in the Camp Creek catchment of central Westland (Reif & Allen, unpublished), nothing is known of the phytosociology of such prominent lichen genera as *Pseudocyphellaria*, *Psoroma*, *Menegazzia*, *Lobaria*, *Sphaerophorus*, *Sticta*, and *Usnea* in a New Zealand setting. Several ecological factors, either singly or in combination, such as moisture, light, temperature, altitude, substrate, etc., may influence the distribution of species of *Pseudocyphellaria* in New Zealand, though detailed studies of these parameters have yet to be made.

A major factor controlling the distribution of species of *Pseudocyphellaria* is rainfall, with the richest diversity of taxa being found in forested areas having an annual average rainfall in the range 600–8000 mm. In the very driest areas of New Zealand, such as Central Otago, which has an annual rainfall of *c.* 400 mm or less, species of *Pseudocyphellaria* are uncommon, with only occasional specimens of *P. crocata*, *P. glabra*, and *P. pickeringii* found among rocks in dry grassland or induced steppe. As a general rule, species of *Pseudocyphellaria* prefer mild temperatures and cloudy, foggy, drizzling conditions with high humidity, such as are found in areas of medium to high rainfall, or where the number of rain days is high.

Light is another important factor, with the richest diversity of species found in habitats of moderate to strong illumination, especially at forest margins, at tree-line, and on larger branches of the forest canopy. Species with a cyanobiont (e.g. *P. allanii*, *P. cinnamomea*, *P. dissimilis*, *P. hookeri*) are much more tolerant of shade than species with a green photobiont, indeed *P. cinnamomea* and *P. dissimilis* often comprise the main ground cover in deeply shaded interiors of lowland forests where the ambient light level is very low and the humidity high. These two species, together with *Lobaria retigera* and *Peltigera dolichorhiza*, are the main (often the sole) foliose lichens able to compete successfully with bryophytes under conditions of low illumination in forest interiors. The green photobiont species *P. multifida* also appears to be able to grow in moderately shaded habitats and is often found at the base of forest trees together with *P. billardierei*, *P. glabra*, *P. homoeophylla*, and *P. pickeringii*. The vertical distribution of species *Pseudocyphellaria* on the trunks of forest trees is discussed by Kantvilas (1985) for Tasmanian rain-forest, and a similar and noteworthy gradient of species is seen in many New Zealand forests with often large clones of *P. colensoi*, *P. coriacea*, *P. coronata*, *P. faveolata*, *P. gretae*, *P. lividofusca*, and *P. rufovirescens* augmenting or displacing the basal species mentioned above.

Besides moisture and light, other factors affecting the distribution of *Pseudocyphellaria* in New Zealand are latitude, altitude, and mean annual temperature, with groupings of species being influenced by all of these parameters in varying degrees. For instance, several species are found in mainly northern coastal habitats (e.g. *P. aurata*, *P. carpoloma*, *P. chloroleuca*, *P. montagnei*, *P. poculifera*) which have a mean annual temperature of *c.* 12–17°C, while other species are found in subalpine to high alpine grasslands exposed to a high number of ground frosts and to freezing or subzero temperatures for long periods.

The nature of the substrate, and also the floristic composition of forests may also influence the species of *Pseudocyphellaria* present in particular habitats. For example, species of *Pseudocyphellaria* (and of many other associating lichens) are usually poorly represented on the bark of *Nothofagus fusca*, especially in pure stands of this tree, whereas the species diversity of *Pseudocyphellaria* on the bark of *N. menziesii* and, to a lesser extent, *N. solandri* var. *cliffortioides*, is much greater. The moisture-retaining bark of *Leptospermum* also seems to be a very favourable substrate for species of *Pseudocyphellaria*, especially when illumination and humidity are optimal.

Biogeography

Pseudocyphellaria in the family Lobariaceae Chev., is a primarily Southern Hemisphere cool-temperate genus of *c.* 110 species, with New Zealand (48 species) and South America (*c.* 46 species) being the main present-day areas of specification (Fig. 14).

Biogeography concerns itself with present and past patterns of spatial distribution of life on earth and the means whereby such distributions have come about. Problems of Southern Hemisphere biogeography have concerned botanists, zoologists, and palaeontologists for many years, with interpretations of past and present distribution patterns of certain southern genera, for example *Nothofagus*, attracting considerable discussion and controversy (Craw, 1982, 1985; Heads, 1985; Humphries, 1981, 1983, 1985; Humphries & Parenti, 1986; Melville, 1982; van Steenis, 1971). In lichen-forming fungi, disjunct distributions in many genera parallel disjunctions in other plant and animal groups, and in spite of their polyphyletic origins and dual nature, lichens and their distribution patterns seem capable of conventional biogeographic analysis.

Pseudocyphellaria is one of several lichen genera which have a rich development of species in the Southern Hemisphere but with only one or a few widespread species present in the Northern Hemisphere. Other mainly southern lichen genera with which *Pseudocyphellaria* can be compared include *Menegazzia* (Santesson, 1942; James in Galloway, 1985*b*); *Neuropogon* (Lamb, 1939, 1948, 1964; Walker, 1985); *Placopsis* (Lamb, 1947); *Psoroma* (Jørgensen, 1978; Henssen & Renner, 1981; Henssen *et al.*, 1983; Henssen, 1983; Galloway, 1985*b*); *Siphula* (Galloway, 1985*b*); and *Sphaerophorus* (Sato, 1968; Ohlsson, 1974; Tibell, 1984; Galloway, 1985*b*). Explanations for such southern distributions found in these various genera must be looked for in terms of accepted biogeographical frameworks, with the concepts of plate tectonics, and the accretion and dispersal of terranes being relevant to most arguments.

The idea that the earth is made up of a series of interlocking plates whose geometry has been subject to cyclic geographical rearrangements through geological time is the central hypothesis of plate tectonics. The earth appears to have consisted of a single 'supercontinent' Pangaea, surrounded by 'superocean' Panthalassa in the late Palaeozoic. In the early Mesozoic two major components of this single landmass, Gondwanaland in the south, and Laurasia in the north, were separated by a triangular re-entrant of Panthalassa, the Tethys Sea, of which today's

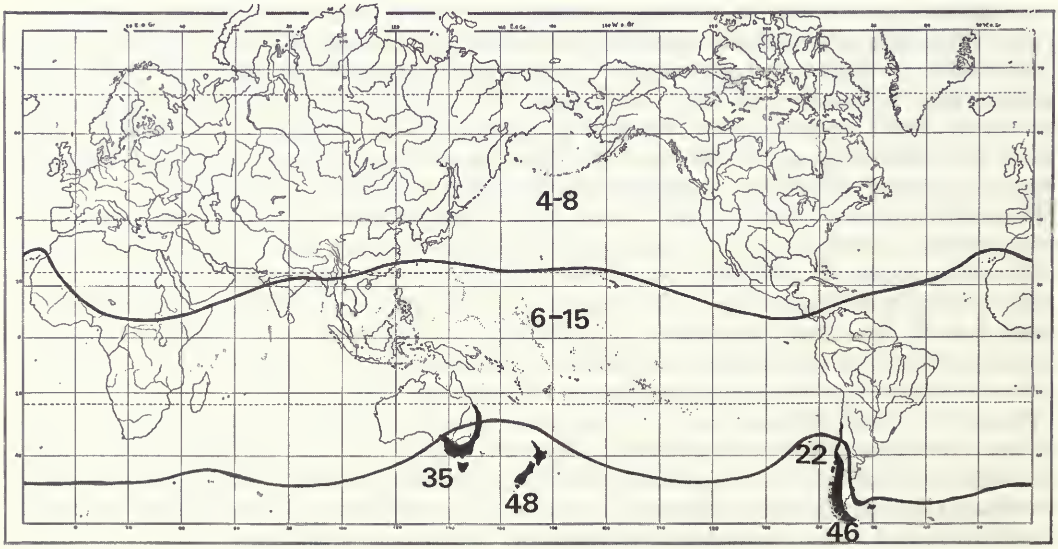


Fig. 14 World distribution of *Pseudocyphellaria* with numbers of species recorded from the cool-temperate Southern Hemisphere (Australia-Tasmania, New Zealand, Juan Fernandez, southern South America), from the tropics, and from the Northern Hemisphere cool-temperate zone.

Mediterranean Sea is the remnant. Warm-temperate, palaeotropical taxa present in Southern Hemisphere biotas derive from organisms that originally populated the Tethyan frontage of Gondwanaland, while cool-temperate taxa were present along the Panthalassic margins of Gondwanaland.

The fragmentation of Gondwanaland and the subsequent movement of its constituent plates is of central importance in discussions of Southern Hemisphere biogeography, and details of the timing of fragmentation and subsequent continental drift of tectonic plates are now fairly well known (e.g. Molnar *et al.*, 1975; Barker & Griffiths, 1977; Weissel *et al.*, 1977; Coleman, 1980; Craddock, 1982; Stevens, 1983; Kamp, 1986). Initial rifting led to the separation of West (South America-Africa), and East Gondwanaland (Antarctica-India-Australia-New Zealand); then followed the separation of South America from Africa with the opening of the southern Atlantic Ocean and the separation of India from Antarctic-Australia.

The separation of the New Zealand microcontinent (including New Zealand, the Campbell Plateau, the Chatham Rise, the Norfolk Ridge, and the Lord Howe Rise – see Fig. 12), itself thought to be of polyphyletic origin (see Howell, 1980), from the Panthalassic margin of Gondwanaland began *c.* 81 million years ago and was completed with the opening of the Tasman Sea (Griffiths, 1971; Hayes & Ringis, 1973; Weissel *et al.*, 1977; Crook & Belbin, 1978; Coleman, 1980; Grindley & Davey, 1982; Cawood, 1984). The final stages in the fragmentation of Gondwanaland were the separation of Australia from East Antarctica (Mutter *et al.*, 1985), the opening of the Drake Passage between Antarctica and South America (Lawver *et al.*, 1985), and the initiation of the circum-Antarctic current (Jenkins, 1964; Kennett *et al.*, 1974; Kennett, 1977, 1979, 1980; Berggren & Hollister, 1977), and the West Wind Drift (Fell, 1962; Close *et al.*, 1978; McDowall, 1978; Fleming, 1979*a*, 1979*b*; Knox, 1979, 1980). Plate tectonics in relation to Southern Hemisphere biogeography is discussed by Melville (1966, 1967); Keast (1971, 1973); Raven & Axelrod (1972); Schuster (1976); and Raven (1979).

Recently the concept of accretion and dispersal of terranes (Nur & Ben-Avraham, 1977, 1982; Kamp, 1980; Howell, 1980, 1985) was used in Southern Hemisphere biogeographical debate (see Craw, 1982, 1983, 1985). Terranes are crustal blocks bounded by faults and not necessarily of uniform composition, which may accrete onto existing continental crust thus introducing new geological (and ? biological) material into a pre-existing formation. New Zealand is thought to be composed of at least four terranes of different origin (Howell, 1980) and it seems that many, if not most, of the circum-Pacific landmasses are also assemblages of unrelated geological taxa (Nur & Ben-Avraham, 1982; Craw, 1985). The terrane concept has thus important consequences for future arguments concerning lichen biogeography (see also Galloway, 1988).

Explanations of Southern Hemisphere biotic distribution patterns fall into two main classes, (1) Dispersal explanations, and (2) vicariance explanations. Dispersal models postulate spread from centres of origin (e.g. Darlington, 1965), a view deprecated by many recent biogeographers (e.g. Croizat *et al.*, 1974; Craw, 1978; Cracraft, 1980; Humphries, 1981, 1983). Vicariance models involve fragmentation of an originally widespread biota into two or more descendant biotas, resulting in the formation of allopatric species (vicariants), the fragmentation involving the formation of a barrier preventing gene flow between the component parts of the originally continuous population (e.g. Rosen, 1978; Nelson & Platnick, 1980*a*, 1980*b*). There is now widespread acceptance of vicariance explanations in the interpretation of Southern Hemisphere biotic distribution patterns (see Brundin, 1966, 1975; Croizat *et al.*, 1974; Cracraft, 1975; 1980; Humphries, 1983), although Craw (1985) strongly advocates use of Croizat's (1958) panbiogeographic methods.

Lichens are an ancient plant group with very slow rates of evolution (Hawksworth, 1982*a*) and were undoubtedly well-developed in cool-temperate Panthalassic Gondwanaland before fragmentation and continental drift. *Pseudocyphellaria* or its progenitors would be present on the cool-temperate vegetation of Panthalassic Gondwanaland, as the high number of vicariant species between New Zealand and South America shows; however, until species from Australia and South America are studied in more detail a biogeographic analysis of the Southern Hemisphere taxa will not be given here.

Five biogeographical groupings or elements are recognized in the New Zealand *Pseudocyphellaria* flora and comprise endemic, australasian, austral, palaeotropical, and cosmopolitan taxa. They are each discussed separately below.

Endemic element

Just over half of the species of *Pseudocyphellaria* found in New Zealand (25 species or *c.* 52%) are endemic and include: *P. allanii*, *P. carpoloma*, *P. corbettii*, *P. coriacea*, *P. crassa*, *P. degelii*, *P. durietzii*, *P. episticta*, *P. fimbriata*, *P. fimbriatoides*, *P. gretae*, *P. homoeophylla*, *P. hookeri*, *P. knightii*, *P. lindsayi*, *P. lividofusca*, *P. maculata*, *P. margaretiae*, *P. montagnei*, *P. murrayi*, *P. nermula*, *P. pubescens*, *P. rufovirescens*, *P. sericeofulva*, and *P. wilkinsii*. Of these taxa, 17 are fertile, primary species without any vegetative propagules, and nine have either isidia or phyllidia as vegetative propagules. Although some taxa are widespread in New Zealand (e.g., *P. coriacea*, *P. homoeophylla*, *P. rufovirescens*), several of the endemics have restricted geographical ranges such as *P. carpoloma*, *P. hookeri*, *P. montagnei*, and *P. sericeofulva* from North I. habitats, while *P. corbettii*, *P. crassa*, *P. maculata*, and *P. nermula* are South I. species. Three species, *P. crassa*, *P. corbettii*, and *P. margaretiae* are best developed in north-west Nelson while the remaining species are more widely scattered.

There is a strong correlation between the distribution of *Pseudocyphellaria* and of *Nothofagus* in New Zealand and most species of *Pseudocyphellaria* are found in lowland to montane beech or beech-podocarp or mixed beech-hardwood forests, with only *P. degelii* and *P. maculata* (together with the austral *P. glabra*) penetrating above tree-line into subalpine to high-alpine grassland. *Pseudocyphellaria* is linked ecologically and evolutionarily with angiosperm phorophytes, especially with *Nothofagus*, and would no doubt have been present in New Zealand, Australia, and South America in the Late Cretaceous and Early Palaeocene at the time of the emergence of the three major groups of beeches, *Nothofagus brassii*, *N. fusca*, and *N. menziesii* (Mildenhall, 1980).

New Zealand's isolation, and the persistence of moist, cool-temperate conditions in both forest and shrubland habitats since the Cretaceous has given rise to many relict plants, from angiosperms to mosses and hepatics (Mildenhall, 1980; J. Wardle, 1984), as well as to many lichens. Although the level of endemism at the generic level is small (Galloway, 1979, 1985*b*) [only *Thysanophoron* in the Caliciales is endemic], at the species level in lichens of Southern Hemisphere genera found in New Zealand, the incidence of endemic taxa is much higher. The most important of these endemic lichens (after species of *Pseudocyphellaria*) are: *Anzia jamesii* (Galloway, 1978*a*); *Argopsis megalospora* (Galloway, 1980*b*); *Austroblastenia pupa* (Sipman, 1983); *Brigantiaea lobulata*, *B. tabacodes* (Hafellner, 1983); *Caloplaca homologa*; *Chaenotheca degelii* (Tibell, 1983); *Collema novozelandicum* (Degelius, 1974); *Cryptolechia myriadella*; *Dendriscocaulon dendroides*; *Haematomma babingtonii*, *H. hilare*; *Hyperphyscia plinthiza*; *Leproplaca lutea*; *Lobaria adscripta*, *L. asperula*, *L. dictyophora*; *Megaloblastenia flavidoatra* (Sipman, 1983); *Megalospora bartlettii*, *M. disjuncta*, *M. gompholoma*, *M. knightii* (Sipman, 1983, 1986); *Melanelia calva, M. glabratuloides* (Esslinger, 1977, 1978); *Menegazzia aucklandica*, *M. dielsii*, *M. foraminulosa*, *M. inflata*, *M. lucens*, *M. pertransita*, *M. pulchra*; *Mycoblastus campbellianus*; *Neofuscelia adpicta*, *N. brattii*, *N. epheboides*, *N. martinii*, *N. melanobarbatica*, *N. minuta*, *N. peloloba*, *N. petriseda*, *N. pictada*, *N. plana*, *N. waiporiensis* (Esslinger, 1977, 1978); *Pannaria periptera*, *P. subimmixta*; *Parmeliella apiculata*, *P. gymnocheila*, *P. mucorina*, *P. neozelandica* (Galloway & James, 1984), *P. thysanota*, *P. variegata*; *Peltularia crassa* (Jørgensen & Galloway, 1984); *Pertusaria allanii*, *P. amaurospora*, *P. circumcincta*, *P. erumpescens*, *P. graphica*, *P. laevis*, *P. lavata*, *P. leucodes*, *P. leucodioides*, *P. melaleucoides*, *P. novaezelandiae*, *P. obvelata*, *P. perfida*, *P. perrimosa*, *P. subverrucosa*, *P. theochroa*, *P. truncata*; *Phlyctella longifera*, *P. megalospora*, *P. oleosa*, *P. sordida*, *P. uncinata*; *Phylisciella aotearoa* (Henssen & Büdel, 1984); *Physcia tenuisecta*; *Placopsis gelidioides*, *P. illita*, *P. lateritioides*, *P. salazina*, *P. subgelida*, *P. subparellina*; *Polychidium contortum*; *Psoroma allorhizum*, *P. athroophyllum*, *P. buchananii*, *P. coralloideum*, *P. euphyllum*, *P. implexum*, *P. melanizum*, *P. xanthomelanum*; *Rinodina cacaotina*, *R. gallowayi*, *R. jamesii*, *R. murrayi*, *R.*

nigricans, *R. otagensis*, *R. peloleuca*, *R. proprior*, *R. subtubulata*, *R. tibellii*, *R. tubulata* (Mayrhofer, 1983); *Sagenidium citrinum* (Follmann, 1975); *Scleromorpha amabilis* (Tibell, 1984); *Siphula dissoluta*; *Sphaerophorus microsporus*, *S. notatus*; *Steinera polymorpha*, *S. radiata*, *S. sorediata* (Henssen & James, 1982); *Stereocaulon colensoi*, *S. fronduliferum*, *S. gregarium*, *S. loricatum* (Galloway, 1980*b*); *Sticta babingtonii*, *S. cinereoglauca*, *S. filix*, *S. lacera*, *S. latifrons*, *S. martinii*; *Thelotrema circumscriptum*, *T. farinaceum*, *T. obovatum*, *T. saxatile*; *Thysanophoron stereocauloides*; *Trapeliopsis colensoi*; *Usnea oncodes*, *U. tenerior*, *U. xanthophana*, *U. xanthopoga*; and *Xanthoria novozelandica*.

The 54% endemism of New Zealand's *Pseudocyphellaria* flora compares with Australia (35 species – endemism 17%), South America (46 species – endemism *c*. 65%), and Juan Fernandez (22 species – endemism 30%) and shows the relatively high level of endemism found in austral populations (Galloway, 1987). In these austral populations and areas of speciation, similar habitats in New Zealand and in South America have a number of vicariant species (i.e. species which are closely related but taxonomically separable) which indicate subsequent evolution after fragmentation and isolation from an originally widely distributed ancestral stock. Thus in subalpine grasslands in New Zealand and in South America, *P. maculata* and *P. lechleri* respectively occupy similar habitats. Other vicariants between New Zealand and South America include *P. degelii*, *P. pickeringii*, and *P. rufovirescens* (New Zealand) with *P. berberina*, *P. flavicans*, and *P. divulsa* in South America.

Australasian element

Twelve species of the New Zealand *Pseudocyphellaria* flora (25%) also occur in Australia, with most shared species being found in south-east Australia and Tasmania, indicating a close floristic and biogeographical relationship of this area with New Zealand. These Australasian taxa are: *P. ardesiaca*, *P. bartlettii*, *P. billardierei*, *P. chloroleuca*, *P. cinnamomea*, *P. colensoi*, *P. coronata*, *P. haywardiorum*, *P. jamesii*, *P. multifida*, *P. neglecta*, and *P. rubella*. Of these taxa, five (*P. ardesiaca*, *P. bartlettii*, *P. colensoi*, *P. haywardiorum*, and *P. rubella*) have soredia, and four (*P. chloroleuca*, *P. coronata*, *P. multifida* and *P. neglecta*) have isidia or phyllidia.

Apart from *P. bartlettii*, *P. chloroleuca*, and *P. haywardiorum* which are shared between northern New Zealand and north-eastern Australia, including Lord Howe I., the bulk of the Australasian species of *Pseudocyphellaria* are found in rain-forest in Tasmania (Kantvilas *et al.*, 1985; Kantvilas & James, 1987) and in Victoria, and in rain-forest and on successional vegetation in New Zealand, although Tasmania has a more depauperate lichen flora at the species level than New Zealand (Kantvilas *et al.*, 1985). For instance, in *Pseudocyphellaria* only 15 species are known from Tasmania (Kantvilas, 1985; Kantvilas & James, 1987), in comparison with 48 species from New Zealand.

There are many similarities in the cool-temperate vegetation of New Zealand and ancient Tasmania, with Gondwanan elements present in both lowland and alpine habitats in both areas (e.g. Burbidge, 1960; Barlow, 1981; Nelson, 1981; Page & Clifford, 1981; Smith, 1981; Kirkpatrick & Brown, 1984). Among the cryptogams, Vitt (1979) records five species of moss common to the Auckland Islands and Tasmania, and Schuster (1982) shows that eight families, and eight genera of hepatics are shared by New Zealand and Tasmania. Numerous lichens (Martin, 1965; Bratt, 1976*a*, 1976*b*, 1976*c*; Bratt & Cashin, 1975, 1976; Galloway, 1985*b*; Kantvilas *et al.*, 1985; Kantvilas, 1985) are also common to New Zealand and Tasmania although the degree of endemism in Tasmanian lichens is low, *c*. 5% (Kantvilas, 1985; Kantvilas & James, 1987). Many of these disjunct taxa are ancient relicts which evolved in Cretaceous times in cool-temperate habitats around the Panthalassic margins of Gondwanaland and which became isolated in cool-temperate habitats on the New Zealand microcontinent and in Tasmania after rifting and drift consequent upon the opening of the Tasman Sea and Bass Strait. New Zealand being isolated from West Antarctica for a greater period of time than Tasmania, possibly experienced a greater variety of more favourable conditions, with opportunities for increased speciation in cool-temperate habitats, with the result that genera such as *Pseudocyphellaria*, *Placopsis*, and *Sphaerophorus* evolved more taxa in New Zealand than in Tasmania. In addition to the relict or palaeoaustral element in the lichen floras of Tasmania and New Zealand (Galloway, 1987*a*; Galloway & Jørgensen, 1987), a distinctive and more recent relationship exists between Australian and New Zealand lichen floras (Galloway, 1979, 1985*b*) with many taxa being transported from sources in Australia to habitats in New Zealand by the prevailing westerly winds (Raven, 1973; Raven & Raven, 1976; Close *et al.*, 1978; Wardle, 1978).

Lichens disjunct between Tasmania, south-eastern Australia, and New Zealand besides the species of *Pseudocyphellaria* already mentioned include *Austroblastenia pauciseptata* (Sipman, 1983); *Bacidia buchananii*; *Baeomyces arcuatus*, *B. heteromorphus* (Galloway, 1980*a*; Kantvilas & James, 1987); *Caloplaca cribrosa* (Poelt & Pelleter, 1984); *Chiodecton colensoi*; *Cladia fulginosa*, *C. inflata*, *C. retipora*, *C. sullivanii* (Galloway, 1977*a*; Filson, 1981*c*); *Cladonia bimberiensis*, *C. murrayii*, *C. neozelandica*, *C. subsubulata*, *C. weymouthii* (Archer, 1985); *Conotremopsis weberiana*; *Degelia durietzii* (Arvidsson & Galloway, 1981); *Dendriscocaulon dendriothamnodes*; *Ephebe fruticosa*; *Gymnoderma melacarpum*; *Hypogymnia billardierei*, *H. kosciuskoensis*, *H. mundata*, *H. turgidula* (Elix, 1979); *Knightiella splachnirima* (Galloway & Elix, 1981); *Lecanora flavopallida*; *Lecidea coromandelica*, *L. laeta*; *Megalopsora atrorubicans*, *M. campylospora*, *M. subtuberculosa* (Sipman, 1983, 1986); *Leioderma amphibolum* (Galloway & Jørgensen, 1987); *Menegazzia aeneofusca*, *M. caliginosa*, *M. castanea*, *M. nothofagi*, *M. testacea*, *M. ultralucens*; *Metus conglomeratus*, *Miltidea ceroplasta* (Hafellner, 1984); *Neofuscelia loxodella*; *Nephroma australe*, *N. rufum*; *Neuropogon acromelanus*, *N. ciliatus*, *N. subcapillaris* (Walker, 1985); *Pannaria crenulata* (Galloway *et al.*, 1983*a*); *Pannoparmelia angustata*, *P. wilsonii* (Galloway, 1978*a*); *Parmelia signifera*, *P. tenuirima*, *P. testacea* (Galloway & Elix, 1983); *Pertusaria nothofagi*; *Phyllopsora congregans*; *Placopsis trachyderma*; *Protoparmelia petraeoides* (Hertel, 1985); *Psoroma asperellum*, *P. caliginosum*, *P. durietzii*, *P. soccatum*; *Psoromidium aleuroides* (Galloway & James, 1985); *Ramalina inflata*; *Roccellinastrum neglectum* (Henssen *et al.*, 1982); *Sagenidium molle*; *Siphula foliacea*, *S. fragilis*; *Sphaerophorus insignis*, *S. macrocarpus*; *Stereocaulon caespitosum*, *S. trachyphloeum* (Galloway, 1980*b*); *Teloschistes fasciculatus*, *T. sieberianus*, *T. velifer*, *T. xanthorioides*; *Thelotrema decorticans*; *Usnea capillacea*, *U. contexta*, *U. torulosa*; *Wawea fruticulosa* (Henssen & Kantvilas, 1985), and see also Galloway (1985*b*).

Austral element

Four species, or *c.* 8% of the *Pseudocyphellaria* flora of New Zealand, belong to this element viz., *P. faveolata*, *P. glabra*, *P. granulata*, and *P. physciospora*. The first three taxa occur widely in southern circumpolar, cool-temperate regions including New Zealand, Tasmania, south-eastern Australia, southern South America, and the various subantarctic island groups scattered in the southern oceans, at latitudes of 45°S or higher; *P. physciospora* also occurs in Juan Fernandez.

Biotas of austral regions have many similarities as well as many disjunct distribution patterns (e.g. Barlow, 1981; Brundin, 1966, 1975; Cracraft, 1975, 1980; Craw, 1984; Darlington, 1965; Dawson, 1958; Fleming, 1979*a*, 1979*b*; Frankel, 1984; Galloway, 1979, 1987*a*; Galloway & Jørgensen, 1987; Godley, 1960, 1975; Jørgensen, 1983; Keast, 1973; Knox, 1979, 1980; McDowall, 1980; Miller, 1982, Moore, 1972, 1979*a*, 1979*b*; Parsons, 1985; Raven, 1979; Raven & Axelrod, 1972; Rich, 1975; Schuster, 1969, 1979; South, 1979; Stevens, 1977, 1980*a*; Vitt, 1979, 1983). Joseph Hooker (1817–1911) was the first to record similarities between lichen floras of New Zealand, Tasmania, the subantarctic islands, and South America (Hooker & Taylor, 1844; Taylor & Hooker, 1845; Hooker, 1847; Galloway, 1985*b*, 1985*c*), and he was also the first to offer a possible explanation of disjunct distributions in southern floras. 'I was led to speculate on the possibility of plants of the Southern Ocean being the remains of a flora that had once spread over a larger and more continuous tract of land than now exists in that ocean; and that the peculiar Antarctic genera and species may be vestiges of a flora characterised by the predominance of plants which are now scattered throughout the southern islands' (Hooker, 1853: xxi). The floristic affinities may be explained in terms of vicariance biogeography (e.g.

Brundin, 1966; Croizat *et al.*, 1974; Craw, 1978; Cracraft, 1975, 1980; Humphries, 1983), or by panbiogeographic analysis (e.g. Croizat, 1958; Craw, 1985).

All three species of *Pseudocyphellaria* are epiphytic on trees or shrubs in lowland to montane forests (*P. glabra* also occurs widely in subalpine scrub and subalpine to high-alpine grasslands) characterized by cool, moist, humid conditions such as may well have existed in cool-temperate regions of the Panthalassic margin of Gondwanaland (Brundin, 1966; Raven & Axelrod, 1972; Arvidsson & Galloway, 1981; Schuster, 1982; Galloway, 1987*a*; Galloway & Jørgensen, 1987).

Two major groupings are found in austral lichen floras (Galloway, 1987*a*), (1) *Palaeoaustral* lichens of which *Pseudocyphellaria faveolata* is an example. These are thought to represent primitive Gondwanan groups poorly adapted for transoceanic dispersal, and which derived from the Cretaceous (or earlier) when the Panthalassic margin of Gondwanaland was available for colonization, where cool-temperate conditions prevailed, and where a vegetated west Antarctic could link South American and South Pacific landmasses. Paleaoaustral lichens show a number of shared features; they grow in cool-temperate environments, often in forests dominated by species of *Nothofagus*, or else in subalpine shrubland or grassland habitats; they are often fertile and generally lack vegetative diaspores; they have been flexible enough to colonize or recolonize cool-temperate habitats during and after periods of climatic deterioration; and they show disjunct distributions. (2) *Neoaustral lichens*, such as *Pseudocyphellaria glabra* and *P. granulata*, are taxa dispersed after the fragmentation of Gondwanaland, mainly post-Pleistocene to the present. They are generally richly provided with vegetative propagules, (isidia in *P. glabra* and soredia in *P. granulata*) which allow long distance transport via, birds, ocean currents or in the West Wind Drift (Raven, 1973; Raven & Raven, 1976; McDowall, 1978; Moore, 1979*b*; Close *et al.* 1978; Galloway, 1979, 1987*a*).

Palaeotropical element

Palaeotropical taxa, in contrast to southern, cool-temperate taxa, have warm-temperate or Tethyan affinities and comprise those organisms shared with ancient Tethys (i.e. the vicinity of the modern Mediterranean) and with its seaway extensions via the Arabian Peninsula, Himalayas, south-west Asia, Indonesia, and New Guinea to the islands of the Pacific (Melville, 1966, 1967). The palaeotropical species *Pseudocyphellaria argyracea*, *P. pickeringii*, *P. dissimilis*, and *P. poculifera* constitute *c.* 9% of the New Zealand *Pseudocyphellaria* flora and range from Madagascar to New Zealand and the islands of the Pacific with an Indo-Pacific, Pacific Plate distribution, analogous to some 50 phanerogamic genera (Good, 1974) including *Cymbidium* and *Nepenthes*, and the hepatic *Paraschistochila* (Schuster, 1979). In New Zealand, palaeotropical species of *Pseudocyphellaria* are associated throughout parts of their range with an assemblage of palaeotropical and amphi-Pacific lichens including: *Anzia madagascarensis* (Galloway, 1985*b*); *Bryoria indonesica* (Jørgensen & Galloway, 1983); *Cetrelia braunsiana*; *Cladonia krempelhuberi*; *Coccotrema cucurbitula*, *C. porinopsis*; *Collema japonicum*, *C. subconveniens*, *C. subfragrans*; *Everniastrum sorocheilum*; *Heterodermia japonica*, *H. microphylla*; *Hypotrachyna ensifolia*, *H. thysanota*; *Laurera cumingii*; *Leioderma duplicatum*, *L. erythrocarpum*, *L. sorediatum* (Galloway & Jørgensen, 1987); *Leprocaulon arbuscula*; *Lobaria retigera* (Galloway, 1981*b*); *Lopadium subcoerulescens*; *Menegazzia eperforata*; *Pannaria gemmascens*; *Peltigera dolichorhiza*, *P. nana*; *Physma byrsaeum*; *Placopsis cribellans*; *Pseudocyphellaria sulphurea* (Galloway, 1985*a*); *Ramalina celastri*; *Sphaerophorus murrayi*; *Sticta sublimbata*; *Thelotrema weberi*; *Thysanothecium scutellatum* (Galloway & Bartlett, 1983); *Turgidosculum complicatulum*; *Usnea maculata*, *U. societatis*; *Xanthoparmelia scabrosa* (Elix *et al.*, 1986).

Cosmopolitan element

Three species (*P. aurata*, *P. crocata*, *P. intricata*) or *c.* 6% of the New Zealand *Pseudocyphellaria* flora have a cosmopolitan distribution, being found on all major landmasses, as well as on oceanic islands in both Northern and Southern Hemispheres. All three species are sorediate and although fertile specimens of all taxa are known, apothecia in *P. aurata* and *P. intricata* are exceedingly rare, and are only occasionally seen in *P. crocata*. While both *P. crocata* and *P.*

intricata have a wide distribution in New Zealand, being known from both cool, moist, shaded, woodland habitats to dry, open, sunny, grassland sites, *P. aurata* is ± restricted to northern coastal habitats north of lat. 37°S.

Discussion

Generic concept and infrageneric classification

Between 1790 and 1890, when Vainio described *Pseudocyphellaria* (Vainio, 1890), many species now recognized in that genus were originally placed in *Sticta* or in several other genera including *Crocodia*, *Nephroma*, *Parmelia*, *Parmosticta*, *Parmostictina*, *Phaeosticta*, *Platysma*, *Pulmonaria*, *Ricasolia*, *Saccardoa*, or *Stictina*. Vainio described *Pseudocyphellaria* for species having pseudocyphellae on the lower surface of the thallus, a distinction which earlier generic descriptions had not emphasized. In his descriptions of *Pseudocyphellaria* and of *Sticta*, Vainio (1890) distinguished anatomical structures of cyphellae and pseudocyphellae, differences which were strengthened over 70 years later by the discovery of a complex medullary chemistry in species of *Pseudocyphellaria*, correlating with the presence of pseudocyphellae. Species of *Sticta* on the other hand, have a notably depauperate medullary chemistry. For most of the 19th century and for at least half of the present century, taxa in *Pseudocyphellaria* were included in *Sticta* (see below), but as we have seen, there are fundamental reasons (viz., the presence of pseudocyphellae, and a richly complex medullary chemistry) for maintaining *Pseudocyphellaria* as an independent genus.

Acharius (1803, 1810, 1814) had a wide generic concept of *Sticta*, including within it species belonging to *Sticta*, *Pseudocyphellaria*, and *Lobaria* 'subtus liberum villosum: cyphellis, sorediis vel maculis interspersis', *cyphellis* being present in *Sticta* sens. str., *sorediis* referring to pseudocyphellae (in *Pseudocyphellaria*), and *maculis* to naked patches on the lower surface often seen in *Lobaria*. Acharius included the following taxa referable to *Pseudocyphellaria*: *Sticta anthraspis*, *S. aurata*, *S. crocata*, *S. obvoluta*, and *S. orygmaea* [= *P. berberina*] (see Galloway & James, 1977; Galloway 1986*a*).

Delise (1825*a*, *b*) also had a wide genus concept of *Sticta*, his monograph of 78 taxa including species now accommodated in *Erioderma*, *Lobaria*, *Pseudocyphellaria*, *Sticta*, and *Xanthomaculina* (Hale, 1985). In his account he included 28 species of *Pseudocyphellaria*, 23 of which he described and figured for the first time (Galloway & James, 1986). Fée (1824–1825) described a new genus, *Delisea*, from King I., Australia, but later changed this name to *Plectocarpon* (Fée, 1824–1825; 1828), since Lamouroux had earlier described *Delisea* in the Rhodophyta. However, it was recently shown that *Plectocarpon* refers to a lichenicolous fungus growing on *Pseudocyphellaria glabra* (Hawksworth & Galloway, 1984).

Link (1833) described a new genus, *Crocodia* for *Sticta aurata*, based on the yellow medulla and pedicellate fruits of that species, and his genus was later taken up by Trevisan (1869) to accommodate species of *Sticta* having a green photobiont and brown, 3-septate spores; however, since then, *Crocodia* was never used at the generic level by any lichenologist. In a study of Brazilian lichens, Martius (1833) made *Sticta* a section of *Parmelia*; however, numerous new species of *Pseudocyphellaria* from explorations in the Pacific and in South America were first described as species of *Sticta* (Montagne, 1835, 1845, 1854, 1856; Meyen & Flotow, 1843; Hooker & Taylor, 1844; Schaerer in Moritzi, 1846; Montagne & v. d. Bosch, 1857).

De Notaris (1851) divided *Sticta* into three unnamed sections based on colour, structure, and presence or absence of cyphellae 'cyphellis urceolatis vel soredii-formibus vel papillaribus, rarius deficientibus praeditus', his concept encompassing *Sticta*, *Pseudocyphellaria*, and *Lobaria* respectively, and being followed by Massalongo (1853). Babington (1855) in his treatment of New Zealand species of *Sticta* proposed three groupings or sections within the genus: 1. *Chrysosticta* Church. Bab., 'cyphellae punctiform, bright golden-yellow' for species of *Pseudocyphellaria*, 2. *Leucosticta* Church. Bab., 'cyphellae white or pale yellow; either punctiform, or explanate, or urceolate', for species of *Pseudocyphellaria* and *Sticta*, and 3. *Pseudos-*

ticta Church. Bab., 'cyphellae wanting altogether, or only occasional', for species of *Pseudocyphellaria* [*P. montagnei*] and *Lobaria*.

Nylander (1854) placed *Sticta* with *Parmelia* and *Physcia* in the tribe Parmeliae but the following year (Nylander, 1855) he refined his concept of the genus to include *Sticta* and *Ricasolia* De Not. (= *Lobaria*), and within *Sticta* he proposed a sectional division viz., 'A. Frons subtus inaequalibus gibberosus, subnudus' [= *Lobaria*], 'B. Frons infra cyphellis praedita albis vel albicantibus' [= *Sticta* pr. p., *Pseudocyphellaria* pr. p.], and 'C. Frons cyphellis citrinis' [= *Pseudocyphellaria*]. Later (Nylander, 1858*a*: 101–103; 1858*b*: 333) he emended his section containing white or whitish cyphellae, to comprise two races viz., 'Stirps *Stictae fuliginosae*' and 'Stirps *Stictae damaecornis*', the former comprising only species of *Sticta* and the latter species of *Sticta* and *Pseudocyphellaria*. In this account, Nylander gave the geographical distribution of taxa and also placed *Sticta coriacea* in *Ricasolia*, a procedure he adopted in all his subsequent accounts of New Zealand lichens (Nylander, 1860*b*; 1866; 1888*b*). In 1860, Nylander's most ambitious and certainly his most detailed work on *Sticta* appeared in Part II of his *Synopsis* (Nylander, 1860*b*). Earlier the same year he described *Stictina* Nyl., to accommodate species with a cyanobiont, his sub-tribe *Stictei* now consisting of three genera, *Stictina*, *Sticta*, and *Ricasolia*, an arrangement he adopted in all subsequent publications dealing with the Lobariaceae (Nylander, 1861*a*; 1861*b*; 1865; 1866; 1868*a*; 1868*b*; 1888*a*; 1888*b*) and which was widely used by later authors (e.g., Hooker, 1867; Hue, 1890, 1901; Jatta, 1890; Stizenberger, 1895; Reinke, 1896). Nylander (1860*a*) first introduced the term pseudocyphellae, and he also described two new genera, *Parmosticta* Nyl. (Nylander, 1875*a*), and *Parmostictina* Nyl. (Nylander, 1875*b*) for taxa with a thalline exciple and ± pedicellate fruits, and a green photobiont, or a cyanobiont respectively. In his *Conspectus synopticus Sticteorum* (1868*b*) Nylander proposed sections *Pseudocyphellatae* Nyl. and *Cyphellatae* Nyl., in both *Sticta* and *Stictina*, a procedure later followed by Hue (1890, 1901), and by Stizenberger (1895).

Müller Argoviensis (1862) divided *Sticta* into two sections, *Eusticta* Müll. Arg. and *Stictina* (Nyl.) Müll. Arg., based on the nature of the photobiont, but in his later accounts of New Zealand lichens (Müller Argoviensis, 1892; 1894, 1896) he followed Nylander's (1860*a*; 1860*b*) use of *Sticta* and *Stictina* as generic names.

Stizenberger (1862) recognized *Sticta*, *Eusticta*, and *Ricasolia* as subgenera of *Sticta* sens. lat., but in his later account of the worldwide distribution of the family Lobariaceae (Stizenberger, 1895) he adopted Nylander's genera based on the nature of the photobiont, retaining *Ricasolia* for species of *Lobaria*, and with species referable to *Pseudocyphellaria* divided between *Stictina* and *Sticta*.

Trevisan (1869) used both spore characters, and the nature of the photobiont to divide *Sticta* into eight genera; *Sticta*, *Stictina*, *Saccardoa* Trevisan, and *Diclasmia* Trevisan all having a cyanobiont, and *Ricasolia*, *Phaeosticta* Trevisan, *Crocodia*, and *Lobaria* having a green photobiont. Species now referred to *Pseudocyphellaria* he included in the following genera: *Stictina* pr. p. (spores brown, 3-septate); *Saccardoa* (spores brown, 1-septate, always pseudocyphellate), *Ricasolia* pr. p. (spores colourless, 1-septate); *Phaeosticta* (spores brown, 1-septate); *Crocodia* pr. p. (spores brown, 3-septate); or *Lobaria* pr. p. (spores colourless, 3-9-septate), and although his generic segregates were adopted in the fungal classifications of Clements (1909) and Clements & Shear (1931), and in the invalid infrageneric classification of the 'order' *Stictales* by Choisy (1960*b*), they have not been subsequently used by any other lichenologists. The use of spore and photobiont characters alone for the delimitation of genera in the Lobariaceae is unsatisfactory and reflects no basic biological differences, since spore colour and septation varies with age of thallus and degree of maturation of the spore.

Vainio (1890) proposed a new classification of the Lobariaceae, comprising the genera *Sticta*, *Lobaria*, and a new genus, *Pseudocyphellaria* Vainio, to accommodate all pseudocyphellate taxa. Vainio placed as synonyms of *Pseudocyphellaria*, Nylander's (1868*b*) *Sticta* sect. *Pseudocyphellatae* and *Stictina* sect. *Pseudocyphellatae*, and Babington's *Sticta* sect. *Chrysosticta* and sect. *Leucosticta*. Within his new genus Vainio recognized four sections, depending on the nature of the photobiont and also on the presence or absence of a thalline exciple (i.e. photobiont cells in the excipular tissue). Sects *Parmosticta* (Nyl.) Vainio and *Parmostictina*

(Nyl.) Vainio, for taxa having a cyanobiont and a green photobiont and a thalline exciple, and sects *Lecidosticta* Vainio and *Lecidostictina* Vainio, for taxa without a thalline exciple and with a green photobiont and a cyanobiont respectively. Vainio's treatment of the Lobariaceae was roundly condemned by Müller Argoviensis (1891: 387) who wrote 'Eigentlich misshandelt und zerfetzt sind die Sticteen', although he allowed that Vainio was correct in synonymising *Ricasolia* with *Lobaria*. Müller stressed that all other taxa in the Lobariaceae should be defined in one of two genera, *Sicta* or *Stictina*, depending on the photobiont present.

Stizenberger (1895), although subscribing to Nylander's arrangement of genera in the Lobariaceae, proposed two new sections, *Leucopseudocyphellatae* Stizenb. and *Xanthopseudocyphellatae* Stinzenb., within the subgen. *Pseudocyphellatae* of both *Sticta* and *Stictina*, the sections being defined by the colour of the pseudocyphellae present.

Hellbom (1896) in his account of the New Zealand lichens collected by Sven Berggren in 1874–75, included species of *Pseudocyphellaria* either in *Sticta* or *Lobaria*, the cyanobiont-containing taxa being placed in *Sticta*, and green photobiont species in *Lobaria*, a rather curious arrangement not subsequently followed by any later author.

In the present century Zahlbruckner, whose views on lichen taxonomy influenced systematic lichenology for nearly 50 years, reverted to Müller Argoviensis's (1862) arrangement of genera in the Lobariaceae, with *Sticta* including both cyphellate and pseudocyphellate taxa, and being divided into sections *Eusticta* and *Stictina* according to the nature of the photobiont (Zahlbruckner 1907; 1925; 1926, 1932, 1941). *Pseudocyphellaria*, although only rarely used in the late 19th century (Malme, 1899; Vainio, 1898*a*, 1898*b*, 1899), was widely used in the present century (see for example Degelius, 1935, 1941; Dodge, 1948, 1964, 1965, 1971; Du Rietz, 1924, 1926; Follmann, 1966; Galloway, 1979, 1983*b*, 1985*a*, 1985*b*, 1986*a*, 1986*b*; Galloway & James, 1977, 1980, 1986; Galloway *et al.*, 1983*b*; Gyelnik, 1931*a*, 1931*b*, 1933, 1938; Huneck *et al.*, 1973; Imshaug, 1950, 1977; Lamb, 1955, 1959; Magnusson, 1940, 1956; Malme, 1934; Magnusson & Zahlbruckner, 1943; Martin, 1965, 1966, 1969*a*, 1969*b*, 1970; Martin & Child, 1972; Räsänen, 1932, 1936, 1937, 1939, 1943, 1944; Renner & Galloway, 1982; Szatala, 1956; Tavares, 1952; Vainio, 1903; Wilkins & James, 1979).

Clements (1909) on the basis of spore colour and septation, and the nature of the photobiont, extended Trevisan's classification of genera within the Lobariaceae to include the following additional pseudocyphellate genera: *Diphaeosticta* Clem., *Diphanosticta* Clem., *Merostictina* Clem., and *Podostictina* Clem. These genera, although recorded in Clements & Shear (1931), were never subsequently used by later lichenologists.

Gyelnik (1931*a*) emended *Pseudocyphellaria* to refer only to taxa with a green photobiont, and he proposed two new sections, *Albidopseudocyphellaria* Gyelnik and *Flavopseudocyphellaria* Gyelnik, for species with white, and with yellow pseudocyphellae respectively. At the same time, cyanobiont-containing taxa formerly included in *Pseudocyphellaria* were referred to a new genus, *Cyanisticta* Gyelnik, comprising sections *Eucyanosticta* Gyelnik, for taxa with white pseudocyphellae, and *Cyanostictina* Gyelnik, for taxa with yellow pseudocyphellae. *Cyanisticta*, although used by several authors (Dodge, 1964, 1965, 1971; Gyelnik, 1931*b*, 1931*c*, 1932, 1938; Räsänen, 1932, 1933, 1936, 1937, 1940, 1943, 1944; Szatala, 1956) is correctly included as a synonym of *Pseudocyphellaria*.

Räsänen (1943) proposed a classification of pseudocyphellate taxa in the Lobariaceae comprising *Pseudocyphellaria* (Vainio) Gyelnik, with two sections, *Parmosticta* (Nyl.) Räsänen, and *Lecidosticta* (Nyl.) Räsänen for species with a green photobiont and with or without a thalline exciple, and *Cyanisticta* and the two corresponding sections *Parmostictina* (Nyl.) Räsänen and *Lecidostictina* (Nyl.) Räsänen, for species with cyanobionts, and with or without a thalline exciple.

Magnusson divided *Pseudocyphellaria* into just two sections, *Leucopseudocyphellatae* (Stizenb.) Magnusson and *Xanthopseudocyphellatae* (Stizenb.) Magnusson, on the basis of the colour of pseudocyphellae (Magnusson & Zahlbruckner, 1943; Magnusson, 1956).

The most recent infrageneric arrangement of *Pseudocyphellaria* appears as part of a rather curious classification of what is called 'Les Stictales' (Choisy, 1960*a*, 1960*b*). Choisy's order Stictales contains four genera, *Heterodea* Nyl., *Sticta*, *Knightiella* Müll. Arg., and *Nephroma*

Ach. The genus *Sticta* is divided into five subgenera viz., *Podosticta* Choisy, *Crocodia* (Link.) Choisy, *Cyphellaria* Choisy, *Pseudocyphellaria* (Vainio) Choisy, and *Lobaria* (Schreber) Choisy, with taxa referable to *Pseudocyphellaria* occurring in subgenera *Podosticta*, *Crocodia*, and *Pseudocyphellaria*. Subgen. *Podosticta* accommodates stalked taxa of both *Sticta* and *Pseudocyphellaria* and has two sections distinguished by the photobiont present, sect. *Eupodosticta* Choisy, having a green photobiont, and sect. *Podostictina* (Clem.) Choisy, based on *Sticta endochrysoides* (Müll. Arg.) Hue [= *Pseudocyphellaria compar* (Nyl.) Magnusson)] with a cyanobiont. Subgen. *Crocodia*, for yellow-medulla species has three sections, sect. *Flavopseudocyphellaria* (Gyelnik) Choisy, and sect. *Hypocrocodia* Choisy [for specimens of *Lobaria*] having a green photobiont, and sect. *Saccardoa* (Trevisan) Choisy with a cyanobiont. Subgen. *Pseudocyphellaria*, Choisy divided into two sections; sect. *Albidopseudocyphellaria* (Gyelnik) Choisy, without a thalline exciple [farther divided into subsect. *Lecidosticta* (Vainio) Choisy, with a green photobiont, and subsect. *Lecidostictina* with a cyanobiont] and Sect. *Parmosticta* (Nyl.) Choisy with a thalline exciple and comprising two subsections; subsect. *Delisea* (Fée) Choisy with a green photobiont [further divided into Stirps *Phaeosticta* (Trevisan) Choisy, with brown spores, and Stirps *Phanosticta* (Clem.) Choisy, with colourless or pale spores] and subsect. *Parmostictina* (Nyl.) Choisy with a cyanobiont. All of Choisy's new names are invalid since they are not provided with Latin descriptions, and his new combinations are also invalid (Art. 33.2) since no basionyms are cited.

Presently it is not considered opportune to elaborate a satisfactory modern infrageneric classification of *Pseudocyphellaria* reflecting evolutionary trends in the genus based on detailed comparisons of anatomy, morphology, chemistry, and biogeography, and pending further studies on Australian, South American, palaeotropical, and tropical taxa, no formal infrageneric arrangement is adopted in the present work. It is hoped, however, that in the near future an acceptable infrageneric classification will be formulated, together with a synoptic key to all known species of the genus.

The genus *Pseudocyphellaria*

Pseudocyphellaria Vainio

in *Acta Soc. Fauna Flora fenn.* **7**: 182 (1890). – *Sticta* subgen. *Pseudocyphellaria* (Vainio) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 124 (1960) comb. inval. (Art. 33.2). Type: *Pseudocyphellaria aurata* (Ach.) Vainio.

Crocodia Link, *Handbuch* **3**: 177 (1833). – *Sticta* subgen. *Crocodia* (Link) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 123 (1960) comb. inval. (Art 33.2). Type: *Crocodia aurata* (Ach.) Link.

Stictina Nyl., *Syn. meth. lich.* **1**(2): 333 (1860). – *Sticta* sect. *Stictina* (Nyl.) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **16**: 371 (1862). Lectotype: *Stictina crocata* (L.) Nyl. [selected by Clements & Shear (1931: 322)].

Phaeosticta Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Sticta* subgen. *Pseudocyphellaria* sect. *Parmosticta*, subsect. *Delisea* stirps *Phaeosticta* (Trevisan) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 125 (1960) comb. inval. (Art. 33.2). Lectotype: *Phaeosticta physciospora* (Nyl.) Trevisan [selected by Choisy (1960: 125)].

Saccardoa Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Sticta* subgen. *Crocodia* sect. *Saccardoa* (Trevisan) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 123 (1960) comb. inval. (Art. 33.2). Lectotype: *Saccardoa crocata* (L.) Trevisan [selected by Choisy (1960: 123)].

Parmosticta Nyl. in *Flora, Jena* **58**: 303 (1875), nom. superfl. (Art. 63.1). – *Pseudocyphellaria* sect. *Parmosticta* (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **7**: 183 (1890). – *Sticta* sect. *Parmosticta* (Nyl.) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 125 (1960) comb. inval. (Art. 33.2). Type: *Parmosticta aurata* (Ach.) Nyl.

Parmostictina Nyl. in *Flora, Jena* **58**: 363 (1875). – *Pseudocyphellaria* sect. *Parmostictina* (Nyl.) Vainio in *Acta Soc. Fauna Flora fenn.* **7**: 183 (1890). – *Cyanisticta* sect. *Parmostictina* (Nyl.) Räsänen in *Acta bot. fenn.* **33**: 12 (1943). – *Sticta* subgen. *Pseudocyphellaria* sect. *Parmosticta* subsect. *Parmostictina* (Nyl.) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 125 (1960) comb. inval. (Art. 33.2). Type: *Sticta hirsuta* Mont.

Diphaeosticta Clements, *Gen. fung.*: 81 (1909). Type: *Diphaeosticta physciospora* (Nyl.) Clements (1909: 175).

Diphanosticta Clements, *Gen. fung.*: 81 (1909). Type: *Diphanosticta cellulifera* (J. D. Hook. & Taylor) Clements (1909: 175).

Merostictina Clements, *Gen. fung.*: 82 (1909). Type: *Merostictina mougeotiana* (Delise) Clements (1909: 175).

Phanosticta Clements, *Gen. fung.*: 81 (1909). – *Sticta* subgen. *Pseudocyphellaria* sect. *Parmosticta* subsect. *Delisea* stirps *Phanosticta* (Clements) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 125 (1960) comb. inval. (Art. 33.2). Type: *Phanosticta freycinetii* (Delise) Clements (1909: 175).

Podostictina Clements, *Gen. fung.*: 82 (1909). – *Sticta* subgen. *Podosticta* sect. *Podostictina* (Clements) M. Choisy in *Bull. mens. Soc. linn. Lyon* **29**: 126 (1960) comb. inval. (Art. 33.2). Type: *Podostictina endochrysoides* (Müll. Arg.) Clements (1909: 175).

Cyanisticta Gyelnik in *Feddes Reprium. Spec. nov. veg.* **29**: 1 (1931). – *Pseudocyphellaria* sect. *Cyanisticta* (Gyelnik) Lamb, in *An. Parq. nac. B. Aires* **7**: 67 (1959) ['1958']. Lectotype: *C. argyracea* (Delise) Gyelnik [selected by Dodge (1964: 168)].

Thallus heteromerous, foliose, dorsiventral, lobate, often very large, orbicular, rosette-forming or irregularly laciniate, or ± dichotomously branched, to complexly entangled, rarely ± monophyllous, loosely to closely attached. *Lobes* very variable, narrow, strap-shaped, ± dichotomously branching with distinctly bifurcating apices which may be pointed, blunt, or rounded, to complex, imbricate. *Margins* entire or variously incised, notched or folded, often conspicuously thickened especially below, often with conspicuous, elongate or verruciform-conical or glomerulate pseudocyphellae, often free and ascending, thick and coriaceous to thin and fragile. *Upper surface* smooth, wrinkled, ± scabrid or hairy, often deeply or shallowly faveolate, with faint or strongly marked reticulum of interconnecting ridges, ridges shallowly rounded to sharply delimited, shining, matt or dull, often conspicuously maculate (× 10 lens, best seen when moist), with or without isidia, pseudoisidia, phyllidia, pseudocyphellae or soredia. *Medulla* white or yellow. *Photobiont* green (*Dictyochloropsis* or *Chlorella*-like) or blue-green (*Nostoc*). *Internal cephalodia* containing *Nostoc* present in taxa with a green photobiont. *Lower surface* glabrous in some taxa but usually ± tomentose, tomentum pale to dark, thick and felted to indistinctly pubescent. *Pseudocyphellae* always present, white or yellow, sparse to frequent, ± immersed in tomentum, plane and ± fleck-like to raised-conical, verruciform or glomerulate, round to irregular, margins distinct or indistinct.

Conidiomata pycnidial (*Lobaria*-type), immersed, ± globose, visible as slight swellings on upper surface and occasionally on lower surface, ostiole dark red-brown to black, plane, elevated or punctate-depressed, randomly scattered or in lines at margins and on thalline ridges, most common towards lobe apices, often eroding and leaving gaping pits. *Conidiogenous cells* colourless, ± cuboid, phialidic, on simple to slightly branched conidiophores, bearing conidia laterally and terminally. *Conidia* colourless, short, baccilliform to slightly dumbbell-shaped.

Ascomata apothecioid, hemiangiocarpic, sessile to pedicellate, laminal or marginal, rounded, margins entire or crenate-striate to ± stellate, with or without phyllidia, isidia or soredia, disc matt or shining, sometimes white-pruinose, thalline exciple in taxa with pedicellate ascomata, smooth to verrucose or areolate-scabrid, hairy, sorediate or maculate; proper exciple in taxa with sessile ascomata, smooth to verrucose or areolate-scabrid or tomentose. Ascomata ascohymenial, hymenium I+ blue, hamathecium of simple, septate, filiform paraphyses, swollen, occasionally ± moniliform, and often pigmented at apices, epithecium present or absent, often pigmented and becoming coloured in K. *Hypothecium* usually pigmented, sometimes changing colour in K. *Asci* shorter than paraphyses, cylindrical or clavate, bitunicate, apex with an I+ blue ring, dehiscence semifissitunicate, the ring everting. *Ascospores* 8 per ascus, uniseriately or biseriately arranged in ascus, colourless or yellow-brown to brown, fusiform-ellipsoid to broadly ellipsoid, rarely acicular-fusiform, apices rounded or pointed, simple at first becoming 1-3 (rarely to 5- or 7-)-septate at maturity, sometimes 2-celled spores have strongly thickened walls with a narrow central canal connecting the locules.

Chemistry: diverse, containing depsides, depsidones, terphenylquinones, pulvinic acid derivatives and triterpenoids of hopane, fernene, stictane or lupane series.

Key to New Zealand species

1a	Medulla white	2
1b	Medulla yellow	39
2a (1a)	Photobiont green	3
2b	Photobiont blue-green	22
3a (2a)	Upper surface pseudocyphellate	4
3b	Upper surface without pseudocyphellae	7
4a (3a)	Lobe margins isidiate or phyllidiate	5
4b	Lobe margins entire, isidia or phyllidia absent	16
5a (4a)	Phyllidia mainly marginal, rarely or never associated with laminal pseudocyphellae; epithecium granular, K + rose pink; spores (27–)32–36(–43) × 7–9 µm	**20. P. episticta** (p. 130)
5b	Isidia terete, marginal and laminal, often associated with laminal pseudocyphellae, at length forming phyllidia at margins; epithecium opaque, yellow-brown, unchanged in K; spores 27–34 × 7–9 µm	**48. P. wilkinsii** (p. 242)
6a (4b)	Lower surface pale buff or whitish; epithecium granular, K + rose pink; spores 30–40 × 7–9 µm	**32. P. lindsayi** (p. 180)
6b	Lower surface dark brown; epithecium opaque, yellow-brown, unchanged in K; spores 25–30 × 7–9 µm	**33. P. lividofusca** (p. 183)
7a (3b)	Sorediate	**24. P. granulata** (p. 152)
7b	Esorediate	8
8a (7a)	Upper surface tomentose or pubescent, or at least at margins	9
8b	Upper surface and margins glabrous	12
9a (8a)	Tomentum on upper surface ± continuous from margins to centre	10
9b	Tomentum or pubescence ± marginal	11
10a (9a)	Lobe margins entire; pseudocyphellae yellow; with a well-defined chemistry	**44. P. pubescens** (p. 228)
10b	Lobe margins phyllidiate or granular-isidiate; pseudocyphellae white; without demonstrable chemistry	**25. P. gretae** (p. 156)
11a (9b)	Lobe margins entire	**12. P. coriacae** (p. 102)
11b	Lobe margins with minutely pubescent phyllidia	**21. P. fimbriata** (p. 139)
12a (8b)	Lobe margins phyllidiate or isidiate	13
12b	Lobe margins entire	17
13a (12a)	Lobe margins phyllidiate	14
13b	Lobe margins isidiate	16
14a (13a)	Lobes rounded; phyllidia dentate-squamiform	15
14b	Lobes entangled-imbricate, narrow, linear-laciniate; phyllidia finger-like to ± coralloid	**37. P. multifida** (p. 199)
15a (14a)	Lower surface wrinkled-bullate or papillate, thinly tomentose; pseudocyphellae inconspicuous; cortex C + red (fugitive)	**36. P. montagnei** (p. 195)
15b	Lower surface ± plane or shallowly wrinkled, ± densely tomentose; pseudocyphellae conspicuous; cortex C –	**11. P. corbettii** (p. 99)
16a (13b)	Lower surface glabrous, shining, pale pinkish white; isidia ± coralloid; medulla C + rose (fugitive)	**8. P. chloroleuca** (p. 85)
16b	Lower surface densely tomentose, chocolate brown or blackish; isidia simple; medulla C –	**23. P. glabra** (p. 146)
17a (12b)	Upper surface plane to undulate	**27. P. homoeophylla** (p. 162)
17b	Upper surface faveolate-impressed	18
18a (17a)	Pseudocyphellae yellow	19
18b	Pseudocyphellae white	20

19a(18a) Lobes elongate; margins with prominent pseudocyphellae ... **7. P. carpoloma** (p. 80)
19b Lobes short, rounded; margins entire, without pseudocyphellae ... **41. P. physciospora** (p. 213)

20a(18b) Lower surface pale, tomentum thin or sparse ... 21
20b Lower surface dark, tomentum thick ... 22

21a(20a) Lobes elongate, dichotomously branched, shallowly faveolate; apothecial disc red-brown; cortex C − ... **46. P. rufovirescens** (p. 235)
21b Lobes rounded, deeply faveolate; apothecial disc black; cortex C + red ... **18. P. durietzii** (p. 126)

22a(20b) Lobes variable, often irregular; margins often indented, with projecting verruciform white pseudocyphellae, not or rarely ridged below; apothecial disc often white-pruinose; medulla containing physciosporin ... **20. P. faveolata** (p. 134)
22b Lobes rather narrow, ± dichotomously branched; margins entire, smoothly rounded, ridged below, without pseudocyphellae; apothecial disc never pruinose; medulla without physciosporin ... **6. P. billardierei** (p. 75)

23a (2b) Upper surface pseudocyphellate ... 24
23b Upper surface without pseudocyphellae ... 25

24a(23a) Pseudocyphellae developing isidia at margins ... **3. P. argyracea** (p. 64)
24b Pseudocyphellae not isidiate ... **31. P. knightii** (p. 177)

25a(23b) Pseudocyphellae white ... 26
25b Pseudocyphellae yellow ... 34

26a(25a) Sorediate ... 27
26b Esorediate ... 29

27a(26a) Upper surface plane or undulate, emaculate; pseudocyphellae of lower surface rare or absent ... **29. P. intricata** (p. 169)
27b Upper surface ± faveolate-reticulate or punctate-impressed, white-maculate (× 10 lens); pseudocyphellae ± prominent below ... 28

28a(27b) Cortex C + red; medulla K + yellow; upper surface reticulate-faveolate; pseudocyphellae below minute, punctiform ... **5. P. bartlettii** (p. 72)
28b Cortex C −; medulla K −; upper surface punctate-impressed; pseudocyphellae below conspicuous, large, ± plane ... **26. P. haywardiorum** (p. 159)

29a(26b) Lobe margins tomentose or pubescent ... **1. P. allanii** (p. 57)
29b Lobe margins glabrous ... 30

30a(29b) Isidiate or phyllidiate ... 31
30b Without isidia or phyllidia ... 32

31a(30a) Isidia mainly terete, glabrous, occasionally ± dorsiventral ... **17. P. dissimilis** (p. 122)
31b Phyllidia pubescent ... **22. P. fimbriatoides** (p. 142)

32a(30b) Upper surface plane; lobes narrow, ± subcanaliculate; lower surface ± strongly costate **9. P. cinnamomea** (p. 91)
32b Upper surface faveolate-impressed; lobes not subcanaliculate; lower surface not costate 33

33a(32b) Lobes rounded, deeply faveolate; cortex C + red ... **28. P. hookeri** (p. 166)
33b Lobes elongate, dichotomously branched, shallowly faveolate; cortex C − ... **38. P. murrayi** (p. 204)

34a (25b) Upper surface tomentose ... 35
34b Upper surface glabrous ... 36

35a(34a) Upper surface densely and uniformly tomentose; margins tomentose; pseudocyphellae of lower surface sunk in tomentum ... **35. P. margaretiae** (p. 191)
35b Upper surface tomentose centrally; margins glabrous, shining; pseudocyphellae of lower surface conical-verruciform, projecting above tomentum ... **47. P. sericeofulva** (p. 239)

36a(34b) Lobe margins phyllidiate ... **39. P. neglecta** (p. 207)
36b Lobe margins entire ... 37

37a(36b) Sorediate .... **15. P. crocata** (p. 113)
37b Esorediate 38

38a(37b) Upper surface maculate (× 10 lens); lobes thin; tomentum pale; mainly terricolous in subalpine grassland, occasionally corticolous .... **34. P. maculata** (p. 187)
38b Upper surface emaculate; lobes thick; tomentum dark; corticolous, never terricolous.... **14. P. crassa** (p. 108)

39a (1b) Photobiont green 40
39b Photobiont blue-green 46

40a(39a) Without soredia, isidia, or phyllidia .... **16. P. degelii** (p. 118)
40b Sorediate, isidiate, or phyllidiate 41

41a(40b) Soredia well-defined 42
41b Soredia absent, isidiate or phyllidiate 44

42a(41a) Soralia marginal; upper surface mainly glabrous 43
42b Soralia laminal; upper surface tomentose .... **45. P. rubella** (p. 231)

43a(42a) Soralia linear, confluent, labriform .... **4. P. aurata** (p. 68)
43b Soralia derived from small, marginal, crowded isidia .... **43. P. poculifera** (p. 224)

44a(41b) Phyllidiate 45
44b Isidiate .... **10. P. colensoi** (p. 95)

45a(44a) Lobes linear-laciniate to irregular; upper surface smooth, plane; apothecial exciple translucent, verrucose-scabrid; acetone extract yellow .... **42. P. pickeringii** (p. 218)
45b Lobes broadly rounded; upper surface faveolate; apothecial exciple concolorous with thallus, coronate, dentate-phyllidiate; acetone extract red-purple... **13. P. coronata** (p. 106)

46a(39b) Sorediate or phyllidiate 47
46b Without soredia or phyllidia .... **30. P. jamesii** (p. 174)

47a(46a) Sorediate .... **2. P. ardesiaca** (p. 61)
47b Phyllidiate .... **40. P. nermula** (p. 210)

The species

1. **Pseudocyphellaria allanii** D. Galloway **Fig. 15**

in *Mycotaxon* **16**: 202 (1982). Type: New Zealand, South I., Canterbury, Mt Peel, on track to Emily Falls, Peel Forest, on fallen *Pseudowintera* on bank of stream, 20 March 1979, *D. J. Galloway* (CHR 343256! – holotype; BM! – isotype).

Morphology: Thallus orbicular to spreading, in ± entangled clones, 8–15(–20) cm diam., corticolous, loosely to closely adnate centrally, margins ± free. *Lobes* linear-elongate, (3–)5–8(–14) mm wide, 1·5–6 cm long, attenuating at apices, apices blunt, rounded or ± furcate, plane or subconvex centrally, often ± canaliculate towards apices, subdichotomously branched, discrete, sinuses prominent, semicircular. *Margins* entire, sinuous, conspicuously ridged and thickened below, occasionally with conspicuous, round, white pseudocyphellae, often ± tomentose. *Upper surface* dark leaden grey or grey-blue suffused brownish at margins when moist, pale greyish fawn tinged brownish or reddish at margins when dry, coriaceous, smooth, matt or minutely wrinkled or pitted in parts, minutely areolate-scabrid near margins, also occasionally patchily white-tomentose towards lobe apices, soredia, isidia, maculae, phyllidia, and pseudocyphellae absent. *Medulla* white. *Photobiont Nostoc. Lower surface* uniformly thickly tomentose from margins to centre, tomentum dense, silky, entangled, occasionally patchily glabrous centrally, pale yellowish buff at margins, dark chocolate brown, grey-brown to ± blackened centrally. *Pseudocyphellae* white, conspicuous, scattered, round to irregular, 0·5–2·5 mm diam., plane to concave with a distinctive raised, narrow rim,

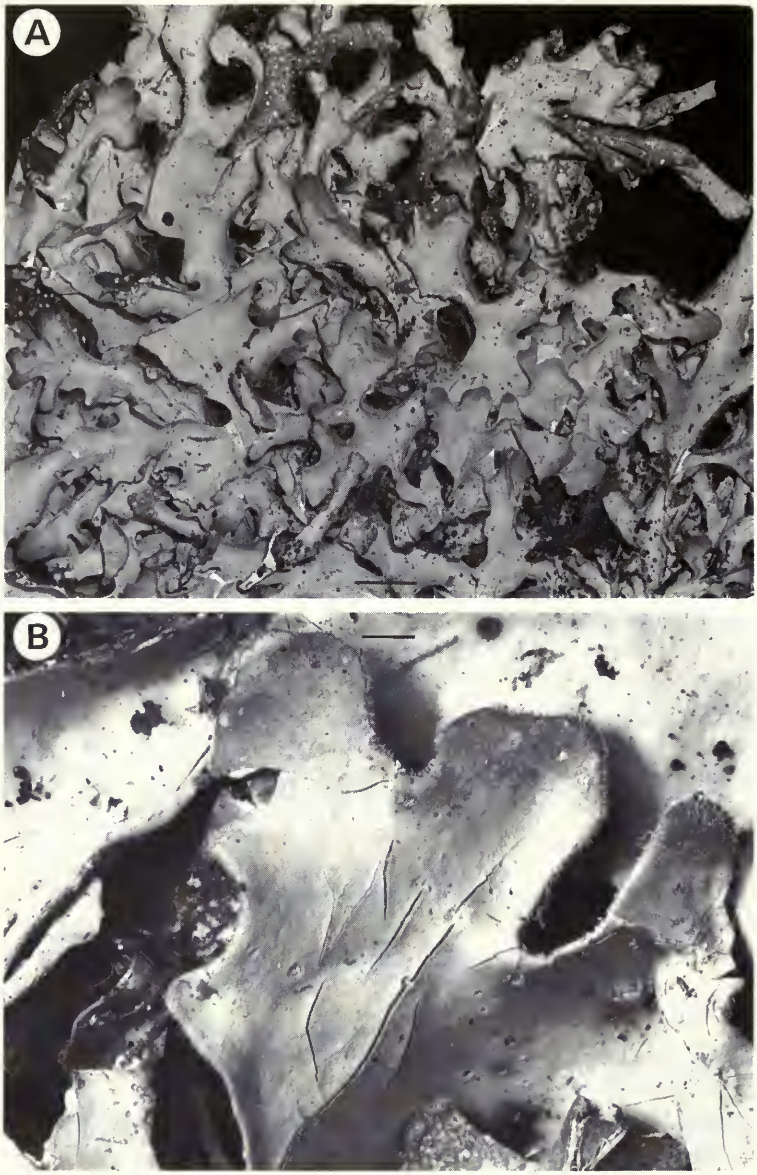


Fig. 15 *Pseudocyphellaria allanii.* Holotype (CHR). A. Scale = 1 cm. B. Scale = 1 mm.

concolorous with lower surface, often sunk in tomentum. *Apothecia* not seen. *Pycnidia* occasional to frequent, at margins and scattered over thallus, singly or in groups, ostiole punctate-depressed, dark red-brown to black, visible on lower surface as hemispherical swellings, 1–1·5 mm diam.

Anatomy: *Thallus* 230–410 μm thick. *Upper cortex* 65–80 μm thick, cells 9–14 μm diam., upper 15 μm straw-yellow, cells compressed, inner 50–65 μm more loosely arranged, cells colourless. *Photobiont layer* 90–140 μm thick, *photobiont Nostoc*, in chains, tightly to loosely clustered, surrounded by a thin gelatinous envelope. *Medulla* 60–150 μm thick, hyphae 3–4 μm diam. *Lower cortex* 30–40 μm thick, colourless to pale straw at outer surface, cells thin-walled 2·5–11·5 μm diam. *Tomental hairs* colourless, 30–230 μm long, in dense clusters.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol(tr.), hopane-15α, 22-diol.

Pseudocyphellaria allanii is named for Dr H. H. B. Allan (1882–1957), first Director of Botany Division, D.S.I.R., who in the 1920s described the vegetation of Mt Peel and later promoted interest in New Zealand lichens (Galloway, 1976).

Distinguishing features: *Pseudocyphellaria allanii* is an endemic species having linear-elongate lobes, and a coriaceous to ± patchily tomentose upper surface, especially towards apices and margins, that is devoid of isidia, phyllidia, pseudocyphellae or soredia. It has a white medulla and a blue-green photobiont, and a densely tomentose lower surface with conspicuous white pseudocyphellae with a distinct, raised, narrow margin at maturity and which resemble true cyphellae. It has a two-hopane chemistry [code A of Wilkins & James (1979)]. It is not known fertile, though small, laminal pycnidia are occasionally produced.

Variation: *Pseudocyphellaria allanii* shows little variation in lobe morphology and appears in the field to be a rather constant species. It occurs rather spasmodically throughout both main islands of New Zealand and is nowhere a common species. It is most closely related to *P. coriacea* and in several localities forms photosymbiodemes with this species (Renner & Galloway, 1982), the chlorosymbiodeme *P. coriacea* developing only on the lower surface and along the margins of the parent cyanosymbiodeme. *P. allanii* is distinguished from *P. coriacea*, a much more widespread and common lichen in New Zealand, only in the nature of the photobiont.

Pseudocyphellaria allanii is readily distinguished from two other endemic non-glabrous species of *Pseudocyphellaria* with blue-green photobionts: (i) *P. margaretiae* D. Galloway, has a ± completely tomentose upper surface, broader, more rounded, and ± imbricate lobes, yellow pseudocyphellae on the lower surface and a more complex chemistry (Galloway *et al.*, 1983*b*), (ii) *P. fimbriatoides* D. Galloway & P. James, has lobes with marginal, tomentose phyllidia, and a much less thickly tomentose lower surface; indeed in many specimens tomentum in this species is greatly reduced or may be often ± absent altogether. It does however have the same chemistry as *P. allanii*.

Distribution: (Fig. 16) *Pseudocyphellaria allanii* is nowhere a common species in New Zealand and is known from Great Barrier I., (Hayward *et al.*, 1986), South Auckland (Kuratau, West Taupo) eastwards to Kuripapango and Lake Waikaremoana, and south to north-west Nelson (Mt Glasgow), South Westland, and South Canterbury (Peel Forest). It has an altitudinal range from near sea-level to subalpine forest at 550 m.

Habitat ecology: *Pseudocyphellaria allanii* is a corticolous species found on the bark of the following phorophytes: *Griselinia littoralis*, *Kunzea ericoides*, *Myrsine australis*, and *Pseudowintera colorata*, in lowland to subalpine forest. It is a species of medium to high-light regimes in standing forest and is found on tree trunks, but not on canopy branches, growing with other lichens and with bryophytes in cool, moist, humid habitats. It is still a rather poorly collected species and is rarely a common or obvious plant, although on a sheltered bench on the eastern slopes of Mt Peel traversed by Allan's Track, a stand of *Myrsine australis* has photosymbiodemes of *P. allanii* and *P. coriacea* as common epiphytes. The two taxa are indistinguishable in the dried state, but when wet the dark grey-blue thalli of *P. allanii* are strikingly apparent. It has also been collected from roadside scrub in South Westland (Fox Bridge).

Specimens examined: North Island. South Auckland: Kuratau, West Taupo, *J. K. Bartlett* (BM, Herb. Bartlett). Gisborne: Lake House, Waikaremoana, 3–4 May 1966, *A. E. Wade* (BM). Hawkes Bay: Kuripapango, 23 August 1981, *J. K. Bartlett* (BM, Herb. Bartlett). South Island. Nelson: Mt Glasgow track, *J. K. Bartlett* 24514*d* (Herb. Bartlett). Westland: Fox Bridge, 7 September 1982, *J. K. Bartlett* 19708 (Herb. Bartlett). Canterbury: Mt Peel, 20, 21 March 1979, *D. J. Galloway* (CHR 343256, CHR 343125).

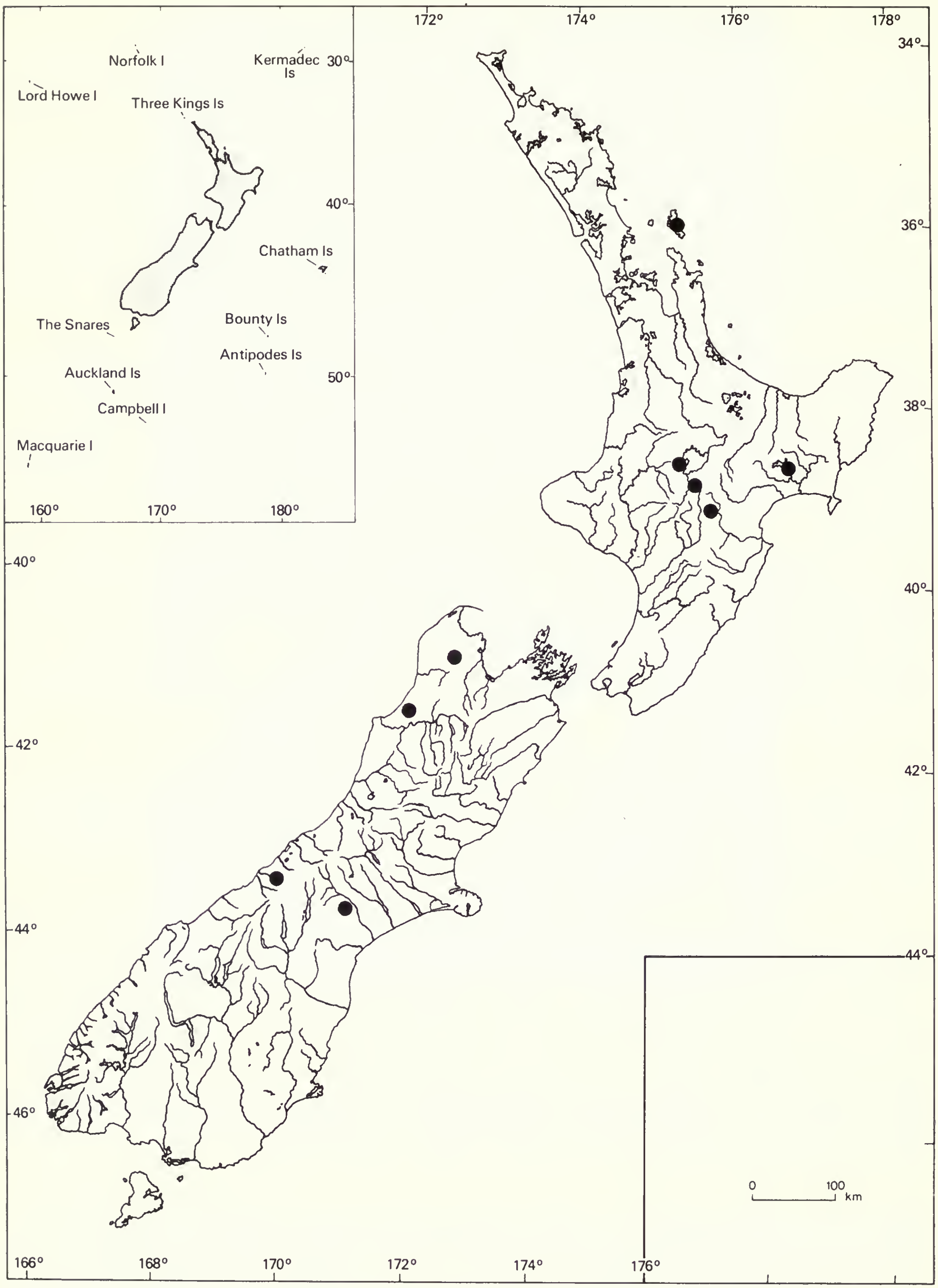

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Fig. 16 Distribution of *Pseudocyphellaria allanii*.

2. Pseudocyphellaria ardesiaca D. Galloway **Fig. 17**

in *Lichenologist* **15**: 141 (1983). Type: New Zealand, South I., Canterbury, Boyle River near Lewis Pass, on bark of *Leptospermum*, on terrace overlooking Boyle Lodge, 9 January 1979, *D. J. Galloway* (CHR 343237! – holotype; BM! – isotype).

Morphology: Thallus ± orbicular, rosette-forming to irregularly spreading, 2–8(–10) cm diam., closely attached over whole of lower surface, ± free at margins, corticolous. *Lobes* rounded, imbricate-convolute, 4–10 mm wide, rarely to 20 mm wide at centre, usually rather short, convex, rarely elongate-laciniate and discrete from margins to centre. *Margins* entire or shallowly notched or incised, slightly thickened below, ± sinuous, sometimes ± downrolled, usually conspicuously sorediate, soralia linear to irregular, sometimes eroding back part of lower surface. *Upper surface* dark slate blue to navy blue tinged yellowish at margins and ridges when wet, glaucous-yellow or pale yellowish buff with a pale grey cast when dry, undulate, smooth, pitted or furrowed to ± plicate-faveolate in parts, shining to minutely scabrid-areolate in parts, occasionally sorediate. *Soralia* linear to irregular at margins, scattered, rounded, ± erose on lamina, soredia yellow to ± blackened, coarsely granular to pseudoisidiate and somewhat gnarled-coralloid, densely clustered in marginal soralia, sometimes parasitized by a fungus and appearing pale to dark red-brown and ± corticate. *Maculae* common on upper surface, best seen when thallus is wet (× 10 lens) forming a ± mottled or marbled pattern of yellow photobiont-free areas on blue upper surface, conspicuous at margins and near thalline ridges. *Medulla* yellow. *Photobiont Nostoc. Lower surface* pale yellow-brown at margins, darkening and often ± blackened centrally, tomentose to margins, tomentum short, ± velvety at margins, woolly, densely squarrose-entangled centrally, pale buff or whitish at margins, brown-black to black centrally, central areas sometimes ± glabrous. *Pseudocyphellae* yellow, scattered, rather sparse at margins, more common centrally, sunk in tomentum near margins, very slightly raised above tomentum centrally, round, ulcerose, 0·05–0·3 mm diam., decorticate area flat or very slightly convex. *Apothecia*. Not seen.

Anatomy: Thallus 180–230 μm thick. *Upper cortex* 34–45(–50) μm thick, uppermost 10–15 μm (2–3 rows of cells) pale straw-coloured, cells round to irregular, 4–7 μm diam., rather flattened compressed, 2–3 rows of cells abutting photobiont layer formed of much larger, more loosely arranged colourless cells 9–15·5 μm diam., with prominent air spaces between cells. *Photobiont layer* (25–)45–60(–70) μm thick, *photobiont Nostoc. Medulla* 45–75 μm thick, hyphae to 4·5 μm thick, encrusted with yellow crystals. *Lower cortex* (15–)20–27 μm thick, cells 4–7 μm diam. *Tomental hairs* developing as budding extensions of cells of lower cortex, at first 5–7(–12) cells, then in fascicles of hyphae (10–12 together) 158–230(–270) μm long, hyphae 5–7 μm thick, walls 1–1·5 μm thick, conspicuously septate, colourless.

Chemistry: pulvinic acid, pulvinic dilactone, calycin, 2α, 3β, 22α-triacetoxystictane, 2α, 3β-diacetoxystictane-22-ol, stictane-3β, 22α-diol(tr.), 2α-acetoxystictane-3β, 22α-diol, 3β-acetoxystictane-2α, 22α-diol, stictane-2α, 3β, 22α-triol.

Distinguishing features: Pseudocyphellaria ardesiaca is an Australasian species having ± closely attached, orbicular or rosette-shaped thalli with short, rounded, convex, somewhat scalloped lobes with sinuous, slightly ascending margins which are often conspicuously sorediate. The upper surface is smooth, occasionally ± areolate-scabrid at the margins, to often complexly rugose centrally and characteristically dark slate blue when moist, often with a conspicuous reticulum of pale yellowish maculae (× 10 lens). Yellow granular soredia are present in linear, sinuous, marginal soralia or scattered on the upper surface (especially towards the lobe apices) as small, ulcerose spots. The medulla is golden yellow with no tendency towards pale or whitish areas, and the photobiont blue-green. The lower surface is pale yellow or brownish with a short, even, rather velvety tomentum, pale yellow or buff at margins, greyish centrally and has scattered yellow pseudocyphellae, either sunk in the tomentum or ± convex and raised above the tomentum. Apothecia are not known.

Variation: Pseudocyphellaria ardesiaca shows rather little morphological variation and is

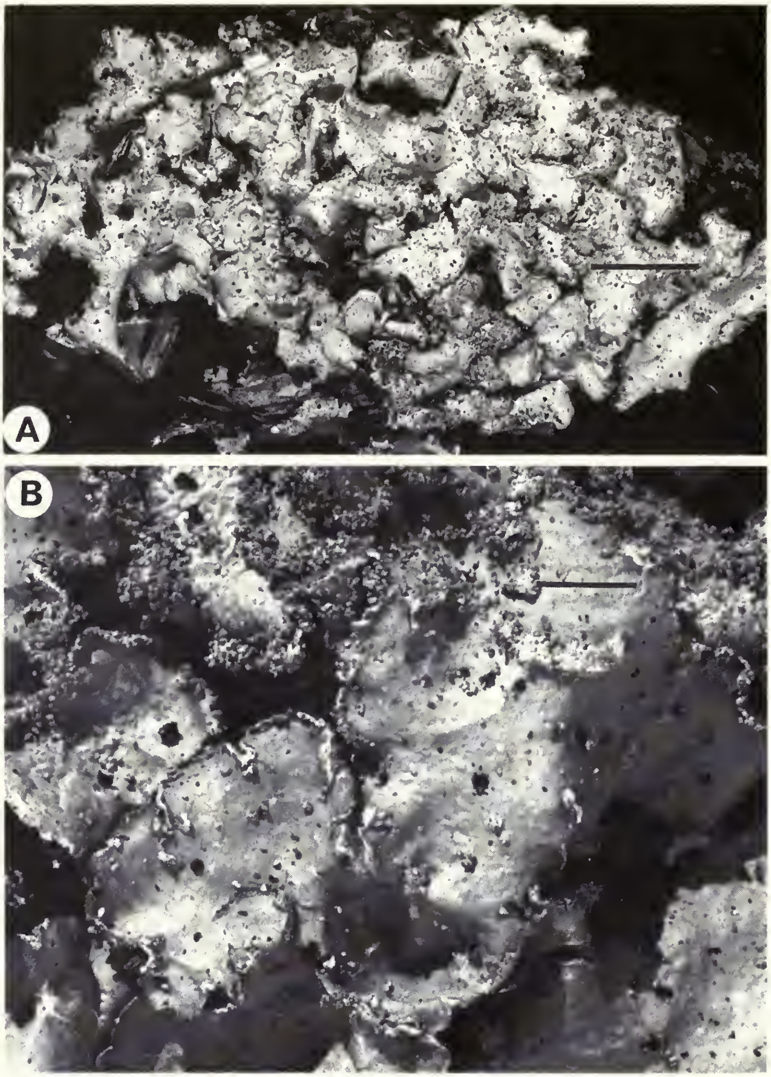

Fig. 17 *Pseudocyphellaria ardesiaca*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 2 mm.

usually a ± tightly adnate, rosette-forming, corticolous species with a degree of variation in the position and density of soredial development. Certain specimens seen have only rather small and widely scattered, discrete marginal soredia, while others may have much or all of the lobe margins copiously sorediate. In most specimens seen, laminal soralia are not especially common, being most obvious towards apices of lobes and only rarely and exceptionally is the upper surface densely covered in soredia. The presence of soredia in *P. ardesiaca* distinguishes it from two related species endemic to New Zealand, *P. jamesii* which is non-sorediate and *P. nermula* which has marginal phyllidia. *P. jamesii* has, in addition, rather narrower, more linear lobes than either *P. ardesiaca* or *P. nermula*, and the surface of its lobes is often ± reticulate-faveolate.

Three southern South American taxa are similar to *P. ardesiaca* but are all taxonomically distinct from it. A vicariant South American sorediate species is very similar in many respects to *P. ardesiaca* but it has thinner, more papery lobes which are larger (8–15 cm diam.), more loosely attached to the substrate, irregularly spreading, linear-laciniate to rather ragged, and not

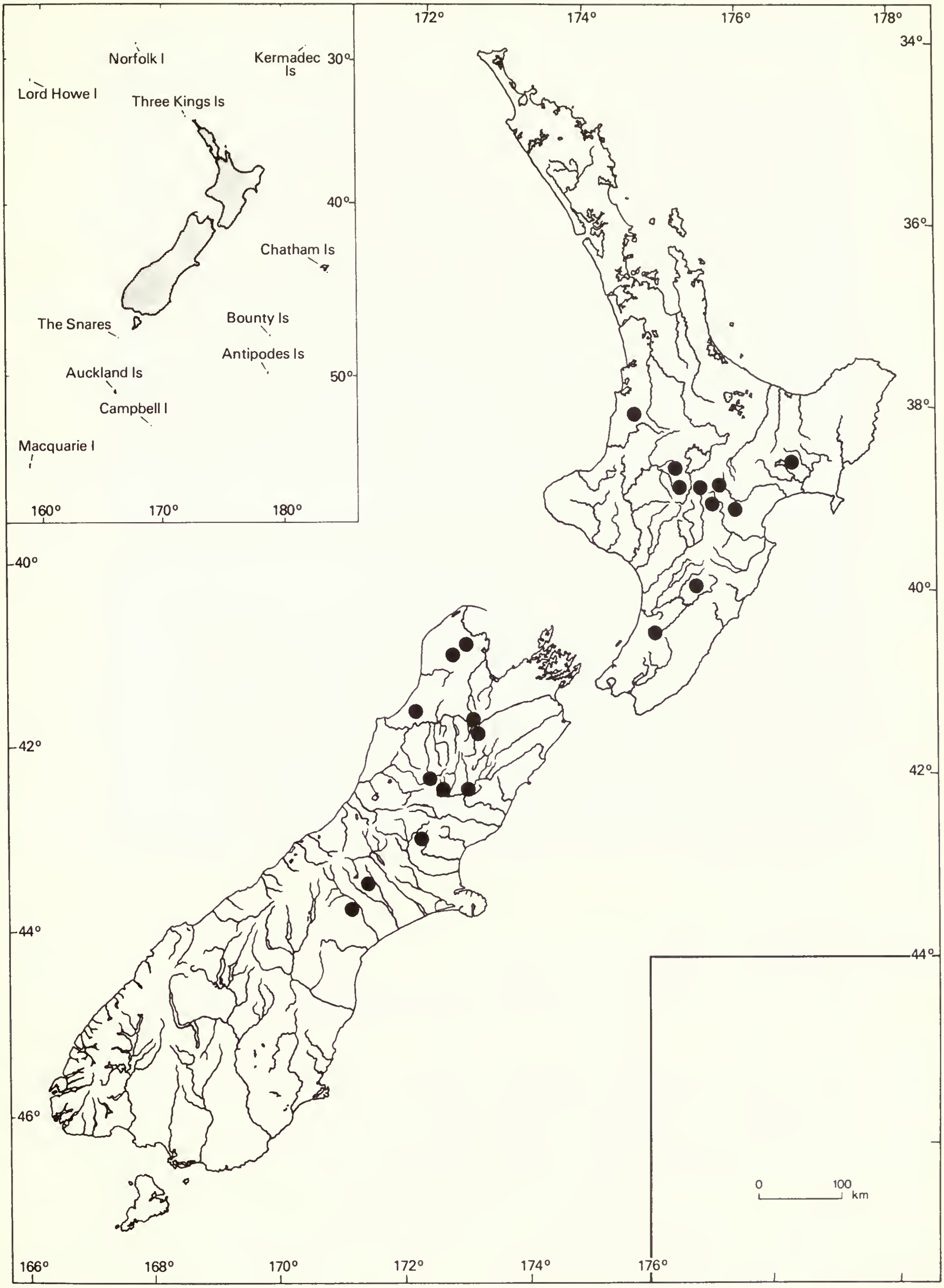
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Fig. 18 Distribution of *Pseudocyphellaria ardesiaca*.

rosette-forming, and with more highly dissected margins. Its upper surface tends to be more distinctly scrobiculate-faveolate, not merely irregularly rugose as in *P. ardesiaca*, and it has prominent and often thickly scattered laminal soralia, with linear, marginal soralia either absent or poorly developed. Its medulla is pale yellow-white rather than uniformly golden yellow as in *P. ardesiaca* and its lower surface is distinctly wrinkled-subbullate with a thin, fine, rather sparse tomentum, and rather sparse, inconspicuous yellow pseudocyphellae (punctate to ± plane, 0·1 mm diam. or less). *P. scabrosa* R. Sant. is distinguished from *P. ardesiaca* by its characteristic scabrid-areolate upper surface and the somewhat glomerulate laminal soralia, and *P. piloselloides* (Räsänen) H. Magnusson differs from *P. ardesiaca* in the longer, ragged, linear-lacinate lobes, the upper surface of which are distinctly reticulate-faveolate, and ± continuously to patchily tomentose (Galloway, 1986*a*).

Distribution: (Fig. 18) From the Mangaotaki River catchment near Pio Pio (South Auckland) eastwards to Lake Waikaremoana, and south to the Tararua Range in North I., and from the mountains of north-west Nelson and northern Westland, and sourthwards mainly east of (though close to) the Main Divide from Lewis Pass, to Mt Peel in south Canterbury, South I. It has an altitudinal range from 200 m to 1350 m. It is known also from south eastern Australia and Tasmania (Kantvilas *et al.*, 1985).

Habitat ecology: *Pseudocyphellaria ardesiaca* occurs on bark or amongst mosses on trunks of the following phorophytes: *Kunzea ericoides*, *Leptospermum scoparium*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, and *Phyllocladus alpinus*. It prefers cool, moist, humid conditions in montane to subalpine habitats and although having a blue-green photobiont it is not tolerant of low-light intensities and is most frequently found at tree-line (Galloway & Simpson, 1978) or lower margins of *Nothofagus* forest (it is most commonly collected from mountain beech, *N. solandri* var. *cliffortioides*), or on the bark of *Leptospermum* in humid scrub associations on river flats, in gullies, or on disturbed ground near recently fired beech forest.

It most frequently associates with other species of *Pseudocyphellaria*: *P. bartlettii* (in the northern part of its range), *P. crocata*, *P. crassa*, *P. degelii*, (usually at tree-line in the mist zone with *Parmelia testacea* and *Usnea capillacea*), *P. fimbriata*, *P. pickeringii*, *P. glabra*, *P. granulata*, *P. gretae*, *P. jamesii*, *P. margaretiae*, *P. nermula*, and *P. rubella*. Elsewhere it associates with the following lichens, most of which are indicators of cool, moist, humid conditions of moderate to high light intensity: *Hypogymnia turgidula*, *Hypotrachyna sinuosa*, *Leioderma applanatum*, *L. sorediatum*, *Menegazzia circumsorediata*, *M. dielsii*, *M. pertransita*, *Nephroma cellulosum*, *N. rufum*, *Normandina pulchella*, *Parmotrema chinense*, *Psoroma durietzii*, *P. leprolomum*, *P. sphinctrinum*, *P. microphyllizans*, *Sphaerophorus ramulifer*, *S. tener*, and *Sticta fuliginosa*.

Specimens examined: 30.

3. **Pseudocyphellaria argyracea** (Delise) Vainio **Fig. 19**

in *Hedwigia* **37**: 35 (1898). – *Sticta argyracea* Delise in *Mém. Soc. linn. Normandie* **2**: 91 pl. 7, fig. 30 (1825). For typification and additional synonymy see Galloway & James (1986).

Morphology: *Thallus* ± rosette-forming, orbicular, 1–5(–10) cm diam., corticolous or saxicolous, closely attached to bark or rocks, loosely attached and ± free when on twigs or amongst moss. *Lobes* irregularly laciniate to broadly rounded, 3–10(–20) mm diam., 1–3 cm long, ± discrete to imbricate. *Margins* sinuous, often slightly revolute and very slightly ridged below, entire or minutely crenate-incised, usually delicately isidiate. *Upper surface* livid grey-blue or grey-black, very minutely mottled (× 10 lens) when moist, pale olivaceous-grey to red-brown when dry, plane, undulate or minutely and irregularly wrinkled, smooth or minutely roughened, fragile, sorediate and isidiate, without maculae or phyllidia. Pseudocyphellae laminal, scattered, punctiform, becoming sorediate, to 3 mm diam., ulcerose, round to irregular, flat to convex, soredia coarsely granular, white. *Pseudoisidia* minute, style-formed, terete, simple to coralloid, at first clustered at margins of pseudocyphellae (Fig. 6A), and at apices and margins of lobes, in some specimens spreading more widely to form a diffract-coralloid crust, dark

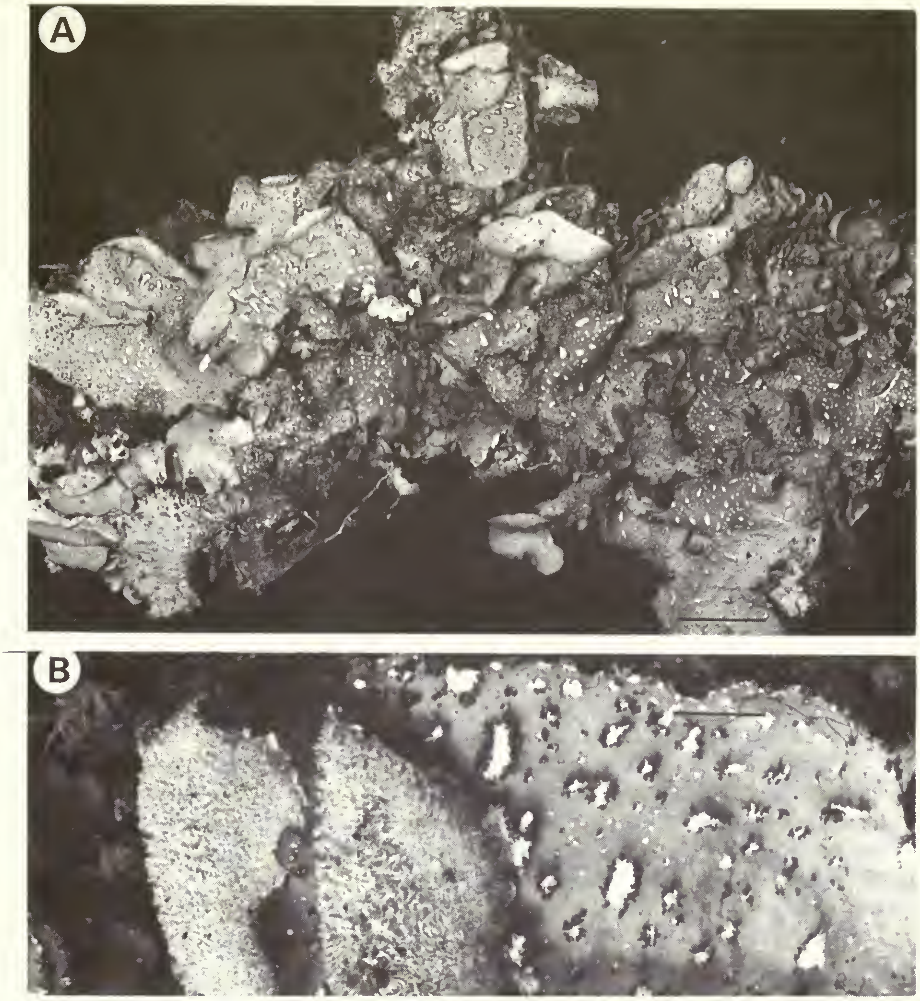


Fig. 19 *Pseudocyphellaria argyracea*. Lake Rotoiti, *Adams* (WELT). A. Scale = 1 cm. B. Scale = 2 mm.

brown, mainly corticate, rarely sorediate below or occasionally forming expanded and flattened regenerating lobules. *Medulla* white. *Photobiont Nostoc. Lower surface* pale fawnish or pinkish white, shallowly wrinkled or pitted, ± densely tomentose from centre to margins, tomentum whitish, silky, entangled, rather shaggy. *Pseudocyphellae* very rare or absent, minute, white, punctiform, best seen near margins. *Apothecia* not seen.

Anatomy: *Thallus* 230–320 µm thick. *Upper cortex* 40–50 µm thick, uppermost 10–12 µm dark brown, remainder straw yellow often with a clear yellow 10 µm zone immediately above photobiont layer, cells thick-walled 4·5–13·5 µm diam. *Photobiont layer* 45–65 µm thick, *photobiont Nostoc*, cells to 4·5 µm diam. *Medulla* 75–140 µm thick, colourless, hyphae 4·5 µm diam. *Lower cortex* 34–45 µm thick, pale straw yellow, cells thicker walled than those of upper cortex, 4·5–14 µm diam, outermost row of cells yellow-brown. *Tomental hairs* to 7µm diam., yellow-brown to red-brown, 100–450 µm long, in clustered fascicles.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol(tr.), hopane-15α, 22-diol, methyl gyrophorate, and gyrophoric acid.

Distinguishing features: *Pseudocyphellaria argyracea*, a widespread, palaeotropical species has a white medulla, a blue-green photobiont, and white pseudocyphellae on the upper and lower surfaces. It is characterized by numerous, laminal, white pseudocyphellae which at maturity become marginally pseudoisidiate with ± corticate, very delicate, finger-like pseudoisidia, concolorous with thallus or darker (often dark brown to brown-black) developed in clusters. In section the pseudoisidia are corticate in their upper parts, being covered by brownish cortical cells continuous with the upper cortex. In some specimens, isidia persist as integral cortical structures and may become ± coralloid, especially at the lobe margins where they are not associated with laminal pseudocyphellae. Very often, isidia associated with laminal pseudocyphellae eventually lose the cortex at the base and become ± sorediate. Such sorediate-pseudoisidiate forms are then often very difficult to separate from specimens of *P. intricata* where occasionally the laminal soredia may become pseudoisidiate and it is possible that a continuum of forms exist between strictly sorediate *P. intricata* and strictly isidiate and laminally pseudocyphellate *P. argyracea*. It has a characteristic two-hopane chemistry [Code A of Wilkins & James (1979)], together with methyl gyrophorate and gyrophoric acid. It is not known fertile.

Variation: In the type locality and throughout the tropics where it is most often collected, *P. argyracea* shows two main growth forms, with lobes being either broadly rounded and ± imbricate, or ± elongate-laciniate and rather narrow, and sometimes with abraded, sorediate margins (Galloway & James, 1986). New Zealand populations are rather similar to the type of *Sticta argyracea* Delise from Réunion, but tend to be rather thinner and more fragile than Mascarene specimens, and rarely in New Zealand does the species form luxuriant colonies such as one finds in early tropical collections, especially those of Bory de St-Vincent made from the type locality.

P. argyracea is related to *P. boryana*, another tropical species with which it is often sympatric, but this latter species differs from it in having narrower, ± subdichotomously branching lobes which are distinctly marginally phyllidiate or isidiate. The laminal pseudocyphellae of this species are also not associated with isidia or pseudoisidia as they are in *P. argyracea.*

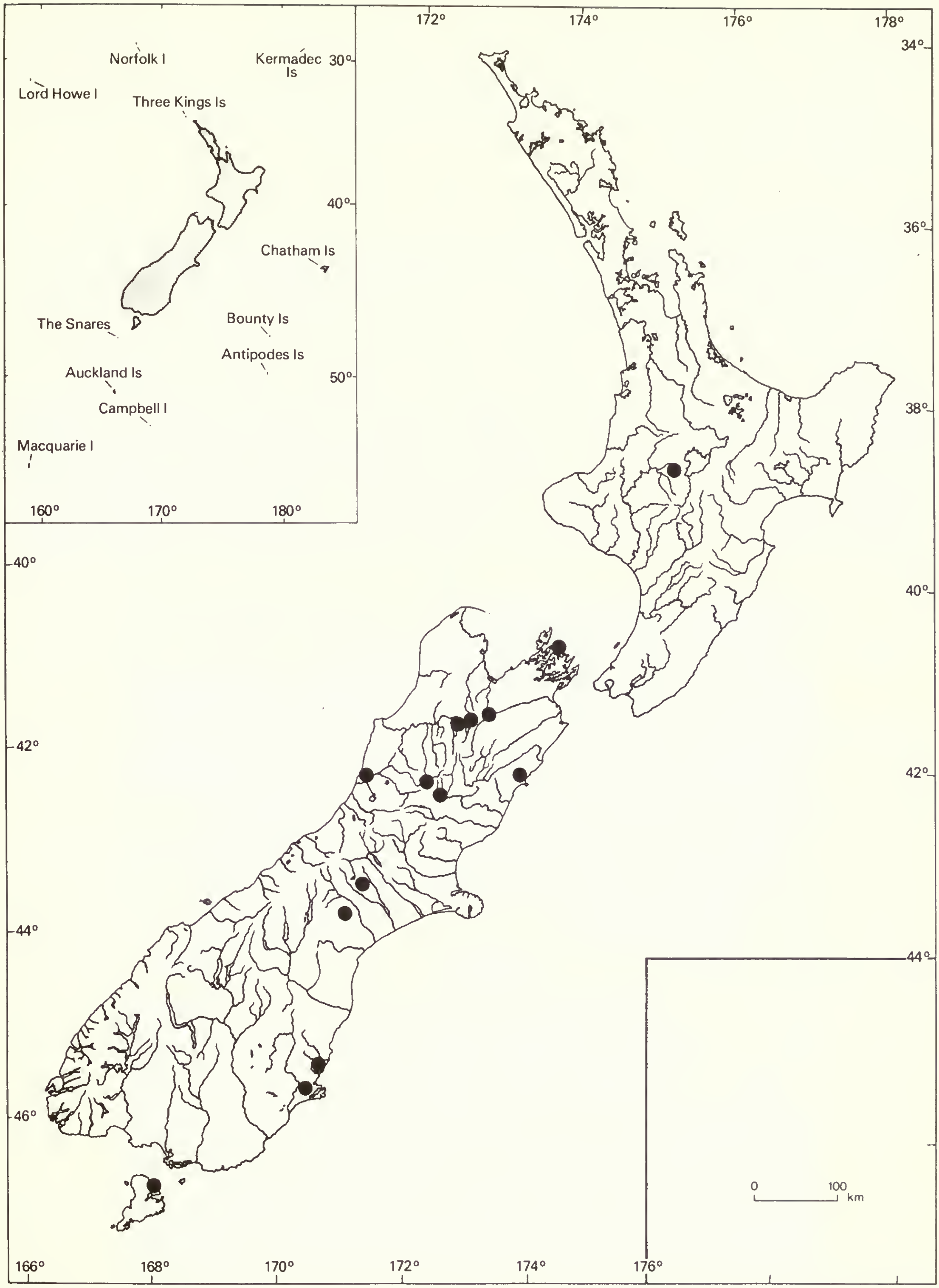
Pseudocyphellaria argyracea is distinguished from *P. intricata* and *P. norvegica* by the delicate isidia or pseudoisidia which are developed both at the margins of the lobes and of the laminal pseudocyphellae. Erosion of isidia associated with the margins of pseudocyphellae in *P. argyracea* can occasionally give rise to pseudoisidiate-sorediate structures which may be very difficult to distinguish from coarsely sorediate strains of *P. intricata* [see above, and also Coppins & James (1979)].

The isidiate Macaronesian-western European species *P. lacerata* differs from *P. argyracea* in several important respects. In *P. lacerata* there are no laminal pseudocyphellae and the isidia are mainly marginal, though occasionally they regenerate from tears or cracks in the upper surface. Isidia are rather nodular and ± terete at first with a conspicuous apical white-frosted tomentum (use × 10 lens), later isidia become glomerulate-coralloid-branched, and may even be somewhat flattened and ± phyllidiate with a pale whitish lower surface and a dark brownish upper surface, also usually with a characteristic whitish tomentum. Densely clustered imbricate marginal isidia in *P. lacerata* appear ± grey-blue [see also Coppins & James (1979)].

The Australasian species *P. haywardiorum* differs from *P. argyracea* in its characteristic punctate-impressed upper surface and the ± bullate lower surface with its prominent, large, raised pseudocyphellae.

Distribution: (Fig. 20) *Pseudocyphellaria argyracea* is still poorly collected in New Zealand, though it appears to be genuinely rare there and apparently does not have the same pattern of distribution as the other widespread, primarily tropical species, *P. aurata.* So far it is known from lat. 39°S southwards to Stewart I., in both lowland and subalpine habitats from sea-level to 600 m.

Habitat ecology: Pseudocyphellaria argyracea in New Zealand is a species of medium – to low-light regimes being found in cool, moist, semi-shaded to deeply shaded habitats on stones or rock, among bryophytes and ferns (*Phymatodes diversifolium*) on the ground, and at or near the bases of forest trees. It is known from the following phorophytes: *Dracophyllum*, *Kunzea ericoides*, *Melicytus ramiflorus*, and *Nothofagus solandri* var. *cliffortioides.* On rock in subalpine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40°
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Fig. 20 Distribution of *Pseudocyphellaria argyracea*.

habitats it associates with *Parmelia signifera*, and elsewhere in its range in New Zealand it grows with the lichens *Normandina pulchella*, *Pseudocyphellaria dissimilis*, *P. glabra*, *P. intricata*, *Sticta fuliginosa*, and *S. limbata*. Its detailed ecological requirements in New Zealand are still poorly understood however. It is a rather thin, fragile species, often growing amongst mosses, with thalli being rather flattened, and when growing on bark, closely appressed.

Specimens examined: 14.

4. Pseudocyphellaria aurata (Ach.) Vainio **Fig. 21**

in *Acta Soc. Fauna Flora fenn.* **7**: 183 (1890). – *Sticta aurata* Ach., *Methodus*: 277 (1803). – *Lichen auratus* (Ach.) Sm. & Sowerby, *Engl. Bot.* **33**: tab. 2359 (1812). – *Nephroma aurata* (Ach.) Pers. in Gaudichaud, *Voy. Uranie Bot.*: 202 (1827). – *Crocodia aurata* (Ach.) Link, *Handbuch* **3**: 177 (1833). – *Parmelia aurata* (Ach.) Eschw. in Martius, *Icones pl. crypt.* **2**: 34 (1834). – *Parmosticta aurata* (Ach.) Nyl. in *Flora, Jena* **58**: 303 (1875). – *Lobaria aurata* (Ach.) Kuntze, *Revis. gen. pl.* **2**: 876 (1891). Type: ? England, Devon, sine loco, ex Herb. *Hudson* – label incomplete (H-ACH 1534! – holotype).

Morphology: Thallus in neat rosettes to irregularly spreading, 5–10(–15) cm diam., loosely attached, ± subascendent, undulate at margins, more tightly adnate centrally, corticolous, occasionally terricolous or saxicolous. *Lobes* 3–12(–20) mm wide, 25–40 mm long, irregularly laciniate, ± discrete at margins, becoming imbricate-confluent centrally to ± discrete from margins to centre, occasionally with small, epiphytic thalli of *Normandina pulchella* and species of *Pannaria*. *Margins* sinuous, undulate, ± subascendent, ± entire to slightly notched or scalloped or crenate, slightly thickened below, with punctiform to linear, yellow pseudocyphel-

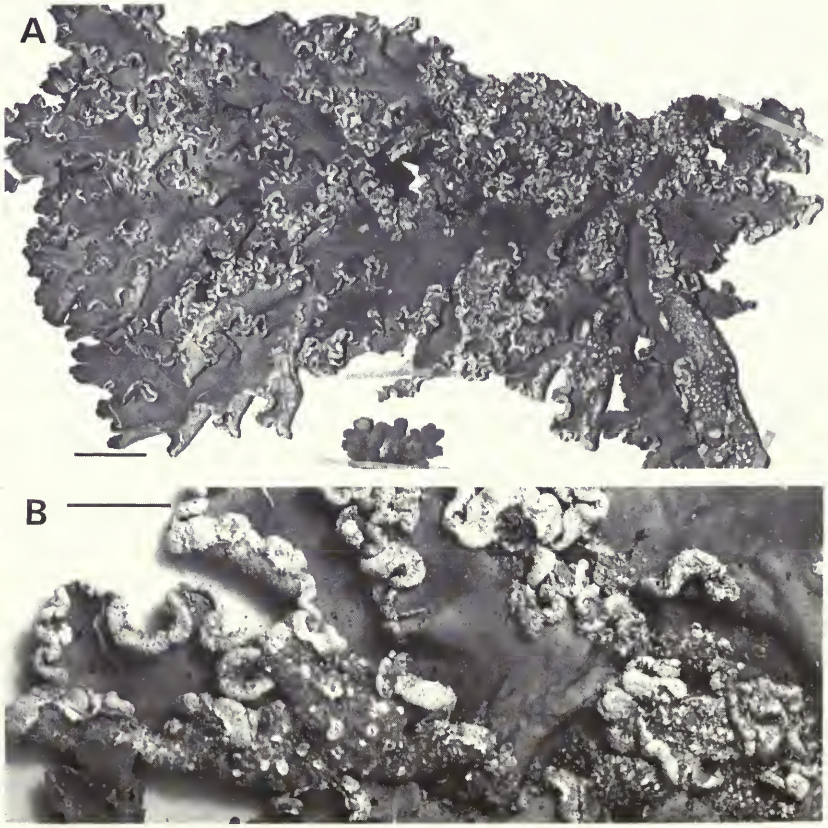


Fig. 21 *Pseudocyphellaria aurata*. Great Mercury Island, *Hayward* H 40.87 (AK 154839). A. Scale = 1 cm. B. Scale = 2 mm.

lae, or more often becoming sorediate, occasionally minutely lobulate with small, regenerating thalline leaflets. *Upper surface* bright lettuce green to a ± dark, fresh green when wet, pale glaucous-grey, olive-brown or buff when dry, often noticeably reddening on storage and becoming brick red to red-brown in the herbarium; undulate, occasionally shallowly to obscurely ridged or pitted in parts, though never truly faveolate, internal cephalodia visible as ± hemispherical swellings; matt, minutely scabrid-areolate in parts, especially near margins which may also be occasionally very finely short-tomentose, to distinctly or delicately pruinose, pruina patchy, thin, white. *Soredia* yellow, coarse, granular often blackened and appearing pseudoisidiate, in primarily marginal, sinuous, labriform soralia which erode conspicuously on the lower surface, also widely scattered at times laminally, in rounded, erose soralia (in favourable conditions a developing sequence from granular soralium to small, corticate lobules differentiating both upper and lower surfaces may be observed). *Isidia*, maculae, phyllidia, and pseudocyphellae absent. *Medulla* yellow. *Photobiont* green, *Dictyochloropsis*. *Lower surface* yellow when wet, rufous, brownish red when dry, dark brown centrally; tomentum rather thin and variable, silky, pinkish buff or whitish at margins, thicker and darker to ± chocolate brown centrally to rather poorly developed and often lacking centrally; shallowly wrinkled-puckered at margins, ± smooth elsewhere. *Pseudocyphellae* yellow, numerous, conspicuous, round to irregular, minute, punctiform especially at margins, 0·5–1·5(–2) mm diam., often confluent centrally, margins very slightly raised, decorticate area flat to shallowly concave, rarely somewhat convex, occasionally with central corticate areas. *Apothecia* rather rare, submarginal to occasionally laminal, solitary, 1–3(–5) mm diam., appearing at first as rounded swellings on upper surface, at length fissuring at the apex to expose concave disc, margins, ragged, yellow-sorediate, distinctly pedicellate, pedicel 1·5–2·5 mm diam., 0·5–1·5(–2) mm tall, slightly narrower than disc and giving fruits a 'waisted' appearance, exciple concolorous with thallus, minutely areolate-scabrid, not hirsute; disc matt, red-brown, imperforate, epruinose, often obscured by overarching sorediate margins; insertion of pedicel distinctly excavate-invaginate on lower surface. *Pycnidia* scattered, occasional, minute, punctiform to ± raised papillate, to 0.1 mm diam., red-brown when wet, black when dry.

Anatomy: *Thallus* (200–)250–350(–450) μm thick. *Upper cortex* colourless, irregularly lumpy, uneven, (40–)45–70(–80) μm thick, cells 5–9 μm diam. *Medulla* loosely interwoven, 85–120 μm thick, brownish yellow, hyphae 4–5 μm thick, densely encrusted with yellow-brown crystals. *Photobiont layer* (45–)55–75(–90) μm thick, cells of *Dictyochloropsis* round to slightly irregular, densely packed, 4·5–7 μm diam., chloroplast occupying most of cell. *Cephalodia* developed between photobiont layer and lower cortex, broady ovoid to ± hemispherical, 100–140 × 90–110 μm, comprising an outer sheath (10–14 μm thick) of periclinal hyphae enclosing a core 80–110 μm thick of thick-walled cells enclosing packets of *Nostoc*. *Lower cortex* 25–37(–45) μm thick, pale straw to ± hyaline, 3–6 rows of cells 6·5–11 μm diam. *Tomental hairs* thick-walled, to 7 μm thick, central canal conspicuous, simple, solitary or in fascicles of 3–6 hyphae together, 45–150 μm long. *Apothecia: Exciple* containing photobiont cells and comprising cortex, photobiont layer, and medulla as in vegetative thallus. *Hypothecium* 45–75 μm thick, opaque, yellow-brown to red-brown, unchanged in K. *Thecium* colourless to pale straw, 55–75 μm tall; *epithecium* red-brown, minutely granular, 7–11·5 μm thick, colour external to tips of paraphyses, unchanged in K. *Asci* very rare, broadly clavate, tapering narrowly at foot, 50–65 μm tall, 13·5–18 μm at widest part. *Ascospores* broadly fusiform-ellipsoid, pointed at apices, 3-septate at maturity, central two locules larger, end locules small and often irregular, distinctly vacuolate, brown, (25–)30–32 × 6–7 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, fernene triterpenoids (A. L. Wilkins, pers. comm.) and unidentified substances.

Distinguishing features: *Pseudocyphellaria aurata* is a cosmopolitan species characterized by a yellow medulla, a green photobiont, yellow pseudocyphellae on the lower surface, and prominent marginal, labriform, ± linear, yellow soralia eroding back the lower surface and containing coarse, granular soredia.

Variation: *Pseudocyphellaria aurata*, an epiphyte of northern coastal forest trees and shrubs, is a fairly constant species showing rather little morphological variation other than differences in lobe dimensions often encountered in ± rosette-forming taxa. There is some variation in the texture of the upper surface especially of the lobe margins where, pruina, scabrosity or laminal cracking may be most evident in some collections, though these features are not always constant in local populations and appear to be influenced by particular microclimatic factors. The laminal, erose soralia are also highly variable in their occurrence and may be ± common to absent altogether. The marginal, sinuous, linear, labriform, yellow soralia are probably the most characteristic and distinguishing feature of this species and are never pectinate-isidiate as they are in the related species *P. poculifera*, which is also much more commonly fertile than *P. aurata*. Occasionally small lobules developing from soralia may be seen in the marginal soralia, less commonly in the laminal soralia, but these are easily distinguished from the coralloid isidia at the margins of *P. poculifera*. The lobes of *P. aurata* are generally broader, thicker, and less incised than those of *P. poculifera*, and there are also differences between the two species in apothecial anatomy (see below under *P. poculifera*).

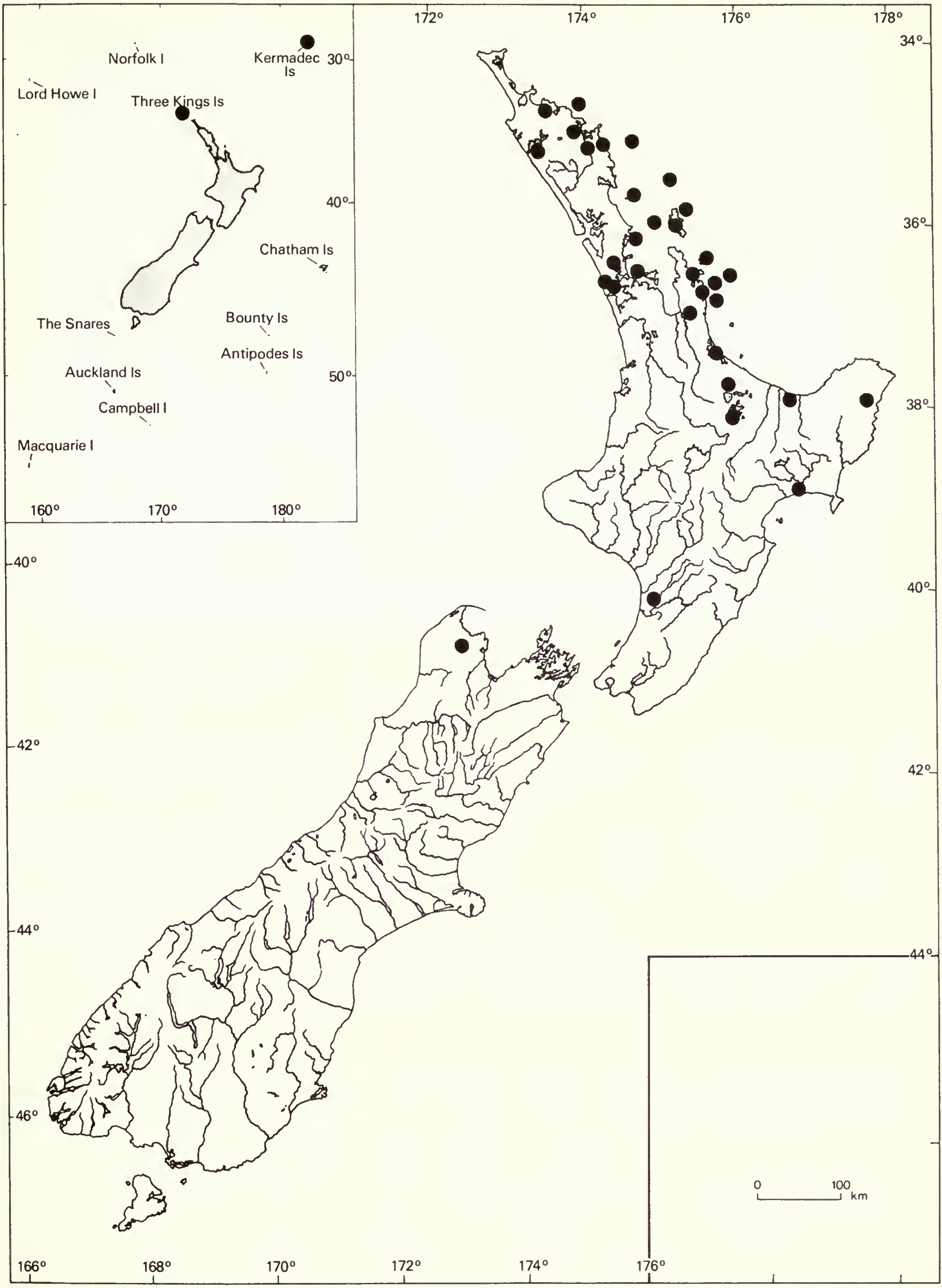
P. pickeringii is distinguished from *P. aurata* by its copious laminal and marginal isidia, its lack of soredia, the massive, corrugate-scabrid apothecial exciple, colourless spores, and a chemistry dominated by stictane triterpenoids. The montane-subalpine *P. rubella* has certain similarities with both *P. aurata* and *P. poculifera* but, although sorediate, it has a distinctive non-glabrous upper surface with development of a characteristic laminal tomentum. Its chemistry is distinct, containing triterpenoids of the lupane series. Specimens of *P. aurata* from some 19th century tropical collections were sometimes misidentified as *Sticta crocata*, this error no doubt deriving from Hoffmann's erroneous use of the name *Platisma crocatum* (L.) Hoffm. [*Descr. pl. cl. crypt.* **2**: 52, tab. XXXVIII figs 1–3 (1794)] for material of *P. aurata* collected by Olof Swartz in the West Indies.

Distribution: (Fig. 22) In mainly coastal habitats from Three Kings Is to Wellington in North I., and a solitary collection from Nelson in South I., sea-level to 500 m. Known from the following offshore islands north of lat. 38°S; Three Kings Is (Great I. and South West I.), Cavalli Is, Poor Knights Is, Hen and Chickens, Rakitu I., Cuvier I., Rangitoto I., Mokohinau I., Little Barrier I., Great Barrier I., Great Mercury I., Red Mercury I., Shoe I., Slipper I., and the Aldermen Is, Tiri Tiri I., Whale I., Penguin I., and Rabbit I.

Habitat ecology: *Pseudocyphellaria aurata* is widespread in both cool-temperate and tropical regions of the world and in New Zealand is characteristic of lowland coastal forest north of lat. 38°S. It will colonize both trunks and twigs of the following phorophytes: *Avicennia marina* var. *resinifera*, *Coprosoma macrocarpa*, *C. rhamnoides*, *Cordyline australis*, *C. kaspar*, *Corynocarpus laevigatus*, *Gaultheria antipoda*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Litsaea calicaris*, *Melicytus ramiflorus*, *Metrosideros excelsa*, *Myrtus bullata*, and *Sphaeropteris medullaris*. It has also been collected from boulders and obsidian outcrops in grassland, from soil below *Leptospermum* in coastal scrub, and from maritime rocks. It is a photophilous species in areas having high summer temperatures and medium to low rainfall where a proportion of the precipitation is as mist or fog. Although primarily a northern species and best represented in North Auckland habitats, *P. aurata* has been able to extend its range beyond the biogeographical barrier of the Auckland isthmus (during higher sea levels of interglacials the isthmus became a strait, isolating North Auckland as an island), through production of soredia.

Pseudocyphellaria aurata associates in northern habitats with the following lichens: *Coccocarpia erythroxyli*, *C. pellita*, *Leioderma duplicatum*, *L. pycnophorum*, *L. sorediatum*, *Normandina pulchella*, *Pannaria elatior*, *P. fulvescens*, *P. periptera*, *Parmotrema crinitum*, *P. cristiferum*, *P. reticulatum*, *P. tinctorum*, *Pseudocyphellaria carpoloma*, *P. chloroleuca*, *Ramalina australiensis*, *Sticta squamata*, and *Teloschistes flavicans*.

Specimens examined: 65.


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
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40°
50°
160°
170°
180°
172°
174°
176°
178°
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36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 22 Distribution of *Pseudocyphellaria aurata*.

5. Pseudocyphellaria bartlettii D. Galloway **Fig. 23**

in *Lichenologist* **17**: 303 (1985). – *Stictina mougeotiana* f. *isidiosa* Müll. Arg. in *Bull. Herb. Boissier* **4**: 89 (1896). – *Sticta mougeotiana* f. *isidiosa* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ*. **3**: 393 (1925). Type: Australia, Queensland, *Mr Bailey* 739 (G 002234! – lectotype).

Morphology: *Thallus* orbicular, 3–6(–12) cm diam., loosely attached centrally, margins free, corticolous. *Lobes* broadly rounded, discrete to subimbricate, 1–3 cm diam. *Margins* entire to minutely crenate, notched or incised, often copiously sorediate and eroding back onto lower surface, sometimes ± inrolled. *Upper surface* dark leaden or slate blue when wet, with white maculae in well-defined reticulate patterns giving a marbled appearance to thallus (× 10 lens), pale olivaceous-grey, grey-buff or brownish red when dry (maculae much less obvious in dry thalli), weakly to strongly reticulate-faveolate or wrinkled-plicate towards margins, ± undulate to shallowly pitted or wrinkled centrally, matt, rather fragile and papery when dry, sorediate, pseudocyphellate, without isidia or phyllidia. *Soredia* in scattered, laminal erose soralia, 0·2–2 mm diam., becoming confluent and ± linear at margins and along reticulate ridges, brownish or greyish, gnarled-glomerulate, minutely style-formed, pseudoisidiate, ± coarsely granular, becoming eroded-white at maturity, often densely clustered near margins and obscuring lamina. *Pseudocyphellae* occasional, scattered, inconstant, minute, pinprick-like, yellow, on ridges near margins of lobes. *Medulla* white. *Photobiont Nostoc. Lower surface* noticeably bullate, minutely wrinkled or pitted below tomentum, pale yellowish buff and ± glabrous in a narrow zone at margins, or ± uniformly buff or dark red-brown to black, tomentum tufted, rather short, thin or thickly developed, occasionally pale buff, more often brown or black. *Pseudocyphellae* scattered, sparse to moderately numerous, eroded-papillate appearing verruciform, 0·1 mm diam. or less, decorticate area flat, white or very pale cream, level with or slightly embedded in tomentum. *Lichenicolous fungus* rarely present, ascomata discoid, translucent, red-brown, developed among soredia 0·5 mm diam. or less. *Apothecia* not seen.

Anatomy: *Thallus* 130–200(–275 at soredia), µm thick. *Upper cortex 18–24* µm thick, upper 9–11 µm dilute orange-brown or red-brown, cells of upper surface compressed forming a ± necrotic layer, lower 9–13 µm colourless, cells larger, pseudoparenchymatous, of round to irregular ± isodiametric, thick-walled cells 4–6 µm diam. *Photobiont layer* (34–)45(–65) µm thick, *photobiont Nostoc* in irregular clumps 11–22 µm diam.,with interstitial hyphae ramifying in all directions. *Medulla* 45–90(–135) µm thick, erupting through upper cortex as erumpent soralia and carrying aloft scattered clumps of photobiont, hyphae dilute yellow-brown, periclinally arranged, loosely interwoven, encrusted with small crystals. *Lower cortex* (15–)20 (–34) µm thick, dilute yellow-brown, 2–3 rows of cells 4·5–9 µm diam., a narrow zone abutting medulla (4–9 µm) of dark brown, stretched cells appearing periclinally arranged, visible in section as a continuous narrow, brown-black line. *Tomental hairs* pale to dark brown, simple, septate, 4·5–6·5 µm diam., 60–180(–300) µm long, in fascicles, 3–10(–20). *Ascospores* of parasitic fungus colourless, simple, oval-ellipsoid, uniseriate in ascus, 6·8–9·1 × 2·3 µm.

Chemistry: Tenuiorin, methyl gyrophorate, hopane-6α, 7β, 22-triol, stictic, constictic, cryptostictic, and norstictic (tr) acids.

Distinguishing features: *Pseudocyphellaria bartlettii* has a white medulla, a blue-green photobiont, white pseudocyphellae on the lower surface, and marginal and laminal erose soralia containing brownish or greyish, pseudoisidiate to ± coarsely granular soredia. The lobes are broadly rounded and on the upper surface photobiont-free areas are present as well-defined reticulate maculae (× 10 lens). It has a complex chemistry related to that of *P. crocata*, but lacking the yellow pigments calycin, pulvinic dilactone, and pulvinic acid from the maculae, soralia, and pseudocyphellae. *Pseudocyphellaria bartlettii* is named for the late J. K. Bartlett (Galloway, 1987*b*), a distinguished collector of New Zealand lichens.

Variation: In the eight specimens seen, little morphological variation was observed, all individuals from South Auckland to South Canterbury appearing remarkably uniform in gross morphology.

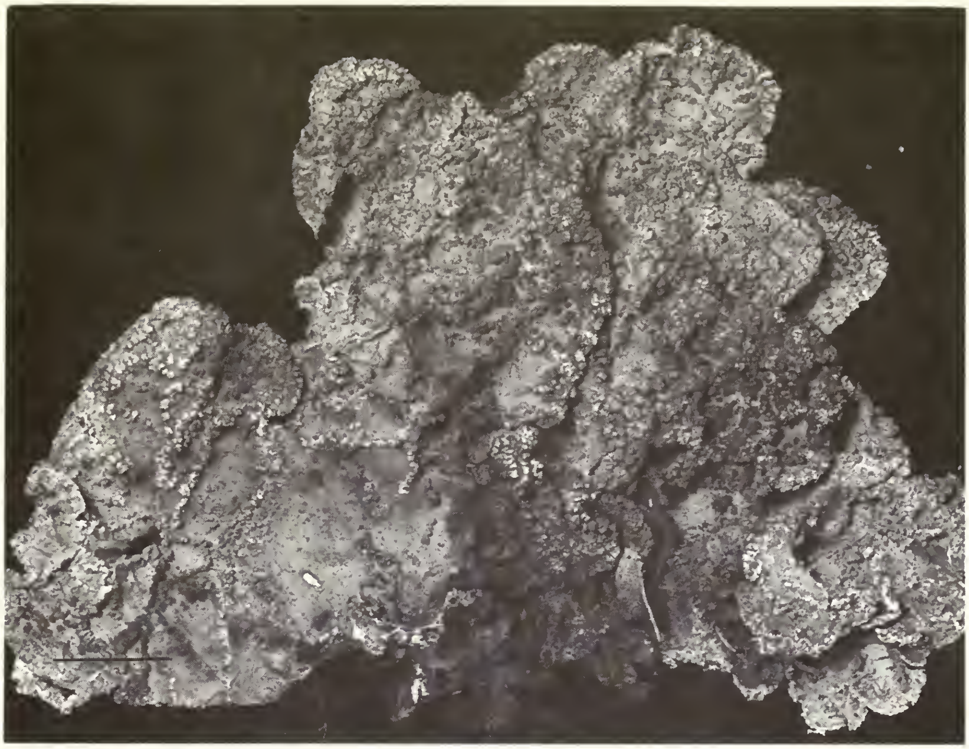


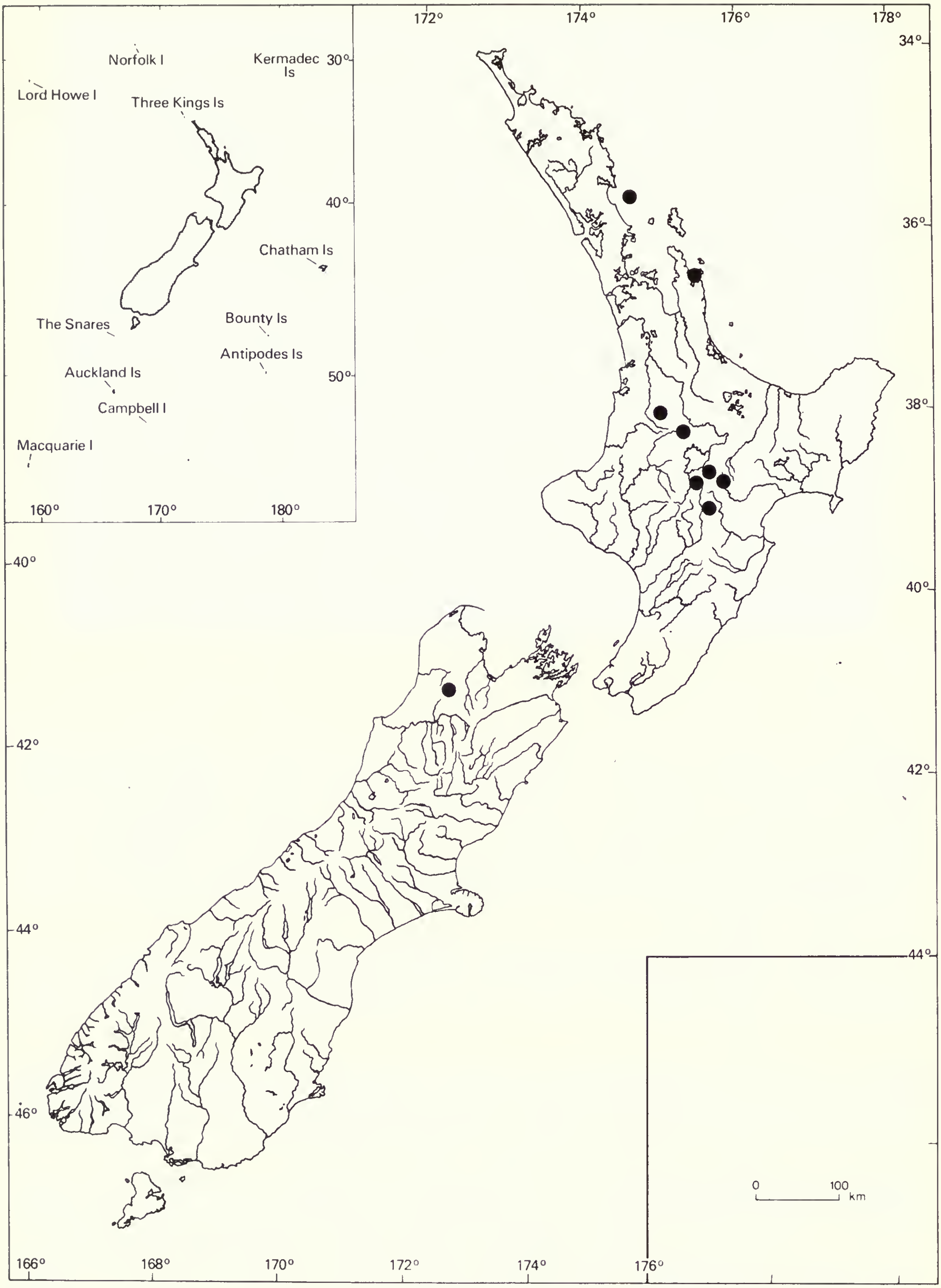
Fig. 23 *Pseudocyphellaria bartlettii*. Rangipo, *Bartlett* 18865 (BM). Scale = 1 cm.

Pseudocyphellaria bartlettii differs from *P. crocata* in lacking yellow pigments in the upper cortex, soralia, and pseudocyphellae, and also in its broad-lobed rosette-forming thallus with a wrinkled-plicate and rather papery upper surface. It differs from *P. neglecta* for the same reasons as well as lacking marginal and/or laminal phyllidia; and it is distinguished from *P. haywardiorum* chemically and morphologically (*P. haywardiorum* has ± laciniate lobes, with a strongly punctate-impressed upper surface, a bullate lower surface with conspicuous, raised pseudocyphellae well delimited from an evenly red-brown to brown-black tomentum; it also has a two-hopane chemistry).

Distribution: (Fig. 24) North I., South of lat. 38°S from near Te Awamutu (South Auckland) to Wellington (Rangipo) and Hawkes Bay (Kuripapango and Kaweka Range). South I., Nelson (Whangapeka Track) to South Canterbury (Mt Peel), 500–1100 m. Known also in eastern Australia (Queensland).

Habitat ecology: *Pseudocyphellaria bartlettii* is still an undercollected species in New Zealand. It forms neat rosettes on the bark of *Leptospermum* in cool, humid, shaded sites and associates with *Heterodermia speciosa*, *Normandina pulchella*, *Pseudocyphellaria ardesiaca*, *P. gretae*, *Parmotrema chinense*, *P. reticulatum*, and *Psoroma sphinctrinum*.

Specimens examined: North Island. South Auckland: Ngaroma, S. of Te Awamutu, 14 July 1979, *J. K. Bartlett* (BM); Waipapa, Tea Tree Bush N. of Mangakino, 12 May 1981, *J. K. Bartlett* (BM). Wellington: Snake Valley S. of Turangi, 11 May 1981, *J. K. Bartlett* (BM); Rangipo, 12 May 1981, *J. K. Bartlett* (BM). Hawkes Bay: Kaweka Range, headwaters of Ngaruroro River, 11 July 1982, *J. K. Bartlett* (BM); Kuripapango, 13 July 1981, *J. K. Bartlett* (BM). South Island. Nelson: Whangapeka Track, Tasman Mountains, 26 January 1980, *J. K. Bartlett* (BM). Canterbury: Deer Spur Track, Mt Peel, 21 March 1979, *D. J. Galloway* (CHR 267113).


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
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166°
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Fig. 24 Distribution of *Pseudocyphellaria bartlettii*.

6. **Pseudocyphellaria billardierei** (Delise) Räsänen **Figs 25, 26**

in *Annls Bot. Soc. zool.-bot. fenn. Vanamo* **2** (1): 39 (1932). – *Sticta billardierei* [‘*Billardieri*’] Delise in *Mém. Soc. linn. Normandie* **2**: 99, pl. 8 fig. 35 (1825). – *Lobaria billardierei* (Delise) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21** (3/13): 41 (1896). – *Sticta faveolata* var. *billardierei* (Delise) Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 278 (1855). – *S. cellulifera* var. *billardierei* (Delise) Hue in *Nouv. Archs Mus. Hist. nat. Paris* III, **2**: 306 (1890). Type: Cap de Van-Diemen (Tasmania), *J.J-H. de la Billardière* (PC-LENORMAND! – lectotype; FI!-isolectotype) [see Galloway *et al.* (1983*b*); Galloway & James (1986)].

Sticta fossulata Dufour in Delise in *Mém. Soc. linn. Normandie* **2**: 99 (1825), nom. nud. (Art. 32·1). – *Crocodia fossulata* Trevisan, *Lichenotheca veneta exs.* 75 (1869) nom, nud. (Art. 32.1). – *Lobaria fossulata* Kuntze, *Revis. gen. pl.* **2**: 876 (1891) nom. nud. (Art. 32.1).

Sticta flotowiana Laurer in *Linnaea* **2**: 40 (1827). – *Pseudocyphellaria flotowiana* (Laurer) Malme in *Bih. K. Svenska Vetensk. – Akad. Handl.* **25** (3/6):22 (1899). Type: Nova Hollandia (Australia), *Sieber* (BM! – lectotype; M! – isotype).

Sticta linearis J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 648 (1844). – *Pseudocyphellaria linearis* (J. D. Hook. & Taylor) Dodge in *Nova Hedwigia* **19**: 489 (1971). – *Sticta fossulata* var. *linearis* (J. D. Hook. & Taylor) Lindsay in *Trans. Linn. Soc. Lond.* **25**: 499 (1866). – *Lobaria fossulata* var. *linearis* (J. D. Hook. & Taylor) Hellbom in *Bih. K. svenska Vetnsk. – Akad. Handl.* **21** (3/13): 41 (1896). Type: Lord Auckland’s Group (New Zealand), *J. D. Hooker* (BM! – lectotype).

Sticta fossulata f. *lacinulata* Krempelh., *Reise Novara Bot.* **1**: 120 (1870). – *S. billardierei* var. *lacinulata* (Krempelh.) Müll. Arg. in *Bull. Herb. Boissier* **2**, App. 1: 36 (1894). – *Lobaria billardierei* var. *lacinulata* (Krempelh.) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21** (3/13): 41 (1896). Type: New Zealand, sine loco, *Jelinek* (M – not seen).

Morphology: Thallus irregularly spreading, somewhat entangled, 5–15(–30) cm diam., corticolous, loosely attached centrally, margins free, often ascending. *Lobes* regularly dichotomously to subdichotomously branched, discrete at margins, ± imbricate centrally, (1–)3–15(–30) mm wide, (1–)3–6(–10) cm long, rather flat, main lobes ± canaliculate, apices truncate, acute or bifurcate. *Margins* entire, slightly to markedly thickened above and below, forming a noticeable ridge on the lower surface, smoothly rounded, without (or very rarely with) projecting pseudocyphellae. *Upper surface* bright lettuce green to glaucous-green when moist, pale grey-green to olive brownish when dry, shallowly to deeply faveolate, main interconnecting ridges well-defined, arcuate, 0·1–0·5(–1·5) mm wide, ± flat, extending across width of lobe, and

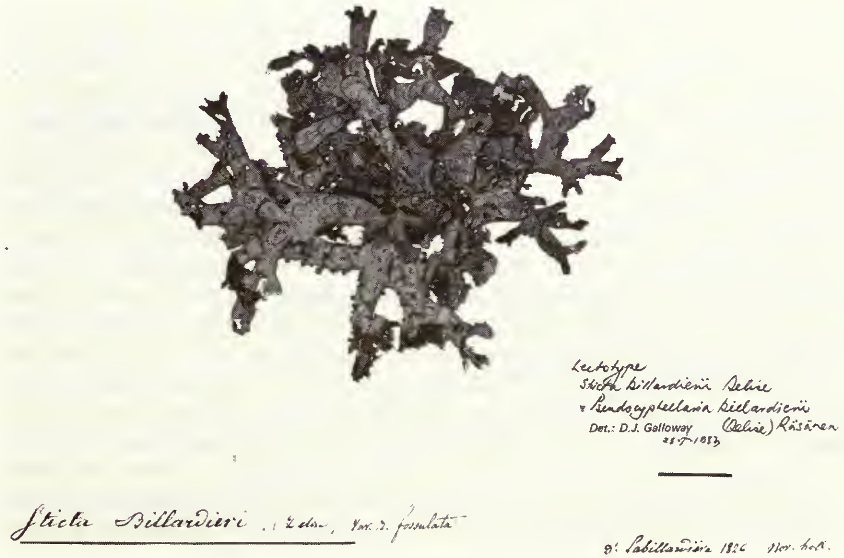
Lectotype
Sticta billardierii Delise
= Pseudocyphellaria billardierii (Delise) Räsänen
Det.: D.J. Galloway 25·V·1983
Sticta Billardieri, Delise, var. β. fossulata
D: Labillardière 1826 Nov. holl.

Fig. 25 *Sticta billardierei*. Lectotype (PC-LENORMAND). Scale = 2 cm.

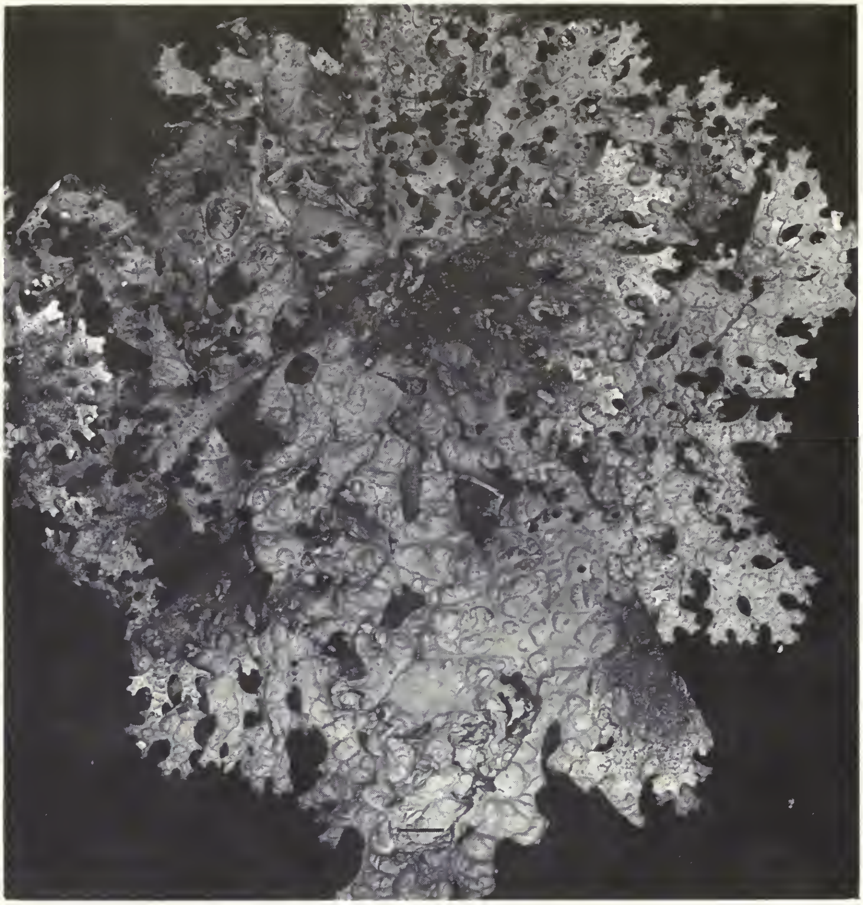

Fig. 26 *Pseudocyphellaria billardierei*. North Egmont, *Tibell* 14967 (UPS). Scale = 1 cm.

dividing lobes into rather large, shallow or deep faveolae, within these secondary, intricating ridges form smaller secondary faveolae, without soredia, isidia, phyllidia, maculae or pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* white or pale buff at margins, darker centrally, conspicuously wrinkled to ± bullate, ± prominently ridged at margins, ± glabrous in a narrow to wide marginal zone, tomentose centrally or from margins to centre, tomentum thin and scattered to dense, wholly, pale whitish or buff and ± velvety at margins, thicker and ± entangled, black or brown centrally. *Pseudocyphellae* white, scattered to frequent, minute, flecklike at margins, 0·05 mm diam. or less, elsewhere to 0·2 mm diam., on interconnecting ridges, raised, verruciform, decorticate area small, depressed-punctate or intented below surrounding margins, rarely flat, margins thin, ± puckered. *Pycnidia* common, in rows or ± clustered at margins and on laminal ridges, minute, punctiform, 0·1 mm or less, red-brown to black, often eroding and leaving small pits. *Apothecia* sparse to moderately common, rather scattered, often more common towards lobe apices, marginal or submarginal, rarely laminal on ridges, solitary to clustered, sessile, constricted at base to subpedicellate, 0·5–5 mm diam., rounded or contorted through mutual pressure, disc dark red-brown to black, shining at first becoming matt, slightly papillate or ± sooty, epruinose, exciple pale yellow-buff to red-brown, translucent and ± colourless when moist, corrugate-scabrid to occasionally ± smooth and shining, rarely pubescent or ± tomentose towards base, obscuring disc in young fruits, restricted to a thin, crenulate or scabrid margin at maturity.

Anatomy: *Thallus* 150–300(–450–500) µm thick. *Upper cortex* 35–45 µm thick, upper parts (9 to 20 µm) yellow-brown, remainder colourless, of densely compacted thick-walled cells, 5–7 µm diam. *Photobiont layer* 22–35 µm thick, *photobiont* green, cells round to irregular 4·5–7 µm diam, closely compacted. *Medulla* 100–300 µm thick, colourless, hyphae to 4·5 µm diam., encrusted with small crystals. *Lower cortex* 20–30(–34) µm thick, uniformly dilute yellow-brown, colour most intense near medulla, cells similar to those of upper cortex, tomental hairs pale yellow-brown, 4–5 µm thick, 20–60(–120) µm long, in fascicles. *Apothecia*: *Exciple* 90–120(–180) µm thick, cellular, outer 20–30 µm dilute yellow-brown otherwise colourless, cells 7–11 µm diam, thick-walled. *Hypothecium* 54–82 µm thick, dilute orange-brown or yellow-brown, opaque. *Thecium* 90–140 µm tall, colourless; *epithecium* dilute red-brown or yellow-brown, dark greenish black in K, 7–13 µm thick, granular in parts, colour external to apices of paraphyses; *paraphyses* simple, apices (2–4 cells) swollen, ± moniliform. *Asci* 70–75 × 15–18 µm. *Ascospores* ellipsoid, thickened 1-septate, brown or grey-brown 25–32(–38) × 9–11.5 µm, septum 4·5–5·5 µm thick.

Chemistry: Tenuiorin, methyl evernate, methyl lecanorate, methyl gyrophorate, evernic and gyrophoric acids, 2″-O-methyl tenuiorin, 2′, 2″-di-O-methyltenuiorin, hopane-6α, 22-diol (zeorin), 6α, 16β-diacetoxyhopan-22-ol, 6α-acetoxyhopan-16β, 22-diol, 6α-acetoxyhopan-23-oic acid, 6α, 22-dihydroxyhopan-23-oic acid, norstictic, stictic, cryptostictic (tr.) and 9-α-acetylconstictic acid (tr.) [Code C of Wilkins & James (1979), see also Galloway *et al.* (1983*b*), Galloway & James (1986), Elix (1986)].

Distinguishing features: *Pseudocyphellaria billardierei* is an Australasian species having linear-elongate, ± dichotomously branching lobes, often widely divergent at their apices and which are conspicuously reticulate-faveolate. Faveolae may be shallow or deep, and the main interconnecting ridges separating them are strongly defined, arcuate, ± flat, and extending across the width of the lobe. Lobe margins are entire, smoothly rounded, without projecting pseudocyphellae and thickened both above and especially below, forming a distinct marginal ridge. The upper surface lacks soredia, isidia, phyllidia, maculae or pseudocyphellae. The species has a white medulla and a green photobiont. The lower surface is wrinkled to ± bullate, pale to brown or blackened, with moderate to dense tomentum and a narrow to broad, glabrous, marginal zone. Pseudocyphellae are white, elevated, verruciform, sometimes with ± puckered margins, and an impressed-punctate decorticate area. Apothecia are primarily marginal, the disc dark red-brown to black and never pruinose. The epithecium turns dark greenish black in K, a characteristic reaction of the species, and ascospores are thickened 1-septate, grey-brown to brown.

Variation: *Pseudocyphellaria billardierei* shows considerable variation in lobe width and length and in complexity of branching, depending on local ecological conditions, though, in general, ± narrow-lobed specimens are more commonly encountered than broad-lobed ones. Specimens with broad lobes tend to be more commonly collected in North Island (especially from Mt Egmont National Park) habitats. The great diversity of lobe form found in *P. faveolata* is not encountered in *P. billardierei*. Very occasionally, depauperate or damaged specimens may develop gnarled-glomerulate to obovoid phyllidia at the margins, but this seems a rare and inconstant condition and is probably a response to particular local adverse conditions. The colour of the upper surface varies with degree of exposure to wind, light or salt-spray, with both coastal scrub and subalpine scrub forms having a noticeably darkened to ± blackened upper (and often also lower) surface. The tomentum of the lower surface also varies from thin, scattered, and poorly developed to thick and entangled, being best developed centrally, with the margins of most specimens examined ± glabrous.

This species is most often confused with *P. faveolata*, both in the field and in the herbarium, however, there are a number of important characters which distinguish the two species. *P. billardierei* has entire, smoothly rounded lobe margins, noticeably ridged below, and without the projecting pseudocyphellae which are characteristic of *P. faveolata*. The apothecia are never pruinose in *P. billardierei* as they are in *P. faveolata* (at least in the youngest fruits) and are usually also less commonly developed. Epithecial pigments in *P. billardierei* turn greenish black in K whereas in *P. faveolata* epithecial pigments turn rose-purple in K. The chemistries of the two taxa are also different, *P. billardierei* being Code C of Wilkins & James (1979) and lacking physciosporin, a metabolite characteristic of *P. faveolata* [Code B of Wilkins & James (1979)]. *Pseudocyphellaria billardierei* is distinguished from *P. physciospora* by differences in epithecium reaction in K, chemistry, and colour of the pseudocyphellae.

Pseudocyphellaria billardierei is distinguished from *P. carpoloma* which has yellow pseudocyphellae (which project at the lobe margins) and a differing chemistry [Code D of Wilkins & James (1979)], and also from *P. rufovirescens* which has a pale, glabrous lower surface and a simple, 2-hopane chemistry [Code A of Wilkins & James (1979)]. Epithecial pigments in both *P. carpoloma* and in *P. rufovirescens* remain unchanged on addition of K to optical sections. See also Table 2 (p. 216).

Ascospores in *P. billardierei* remain thickened 1-septate at maturity, whereas in both *P. carpoloma* and *P. faveolata* both thickened 1-septate and 3-septate spores are routinely found, while in *P. rufovirescens* the spores are never thickened 1-septate, and are pale yellow-brown and not the smoky grey-brown or dark brown of the three other species mentioned (see also Galloway *et al.*, 1983*b*; Galloway, 1985*b*).

Distribution: (Fig. 27) Auckland, Rangitoto I., South Auckland south of lat. 37°S to Southland and also Stewart I., and the Auckland Is (lat. 53°S). Most common in rain-forest areas, especially in South I., both east and west of the Main Divide. Sea-level to 1080 m.

Habitat ecology: *Pseudocyphellaria billardierei* is a large, conspicuous, reticulate-faveolate, ± dichotomously branching lichen, most commonly collected in rain-forest areas of both North and South Islands and on Stewart Island. It is found in beech (*Nothofagus*) forest, conifer (*Dacrydium*, *Dacrycarpus*, *Libocedrus*, *Phyllocladus*, *Podocarpus*, and *Prumnopitys*) forest, and conifer-mixed broadleaf hardwood forest, also in successional stands of *Leptospermum* in fire-altered habitats, and in subalpine and coastal scrub or shrublands (*Dracophyllum*, *Hebe*, *Olearia*, *Senecio*). It is also known from lava blocks on Rangitoto I. Although it reaches an altitudinal limit of 1080 m on *Phyllocladus alpinus* on the Kaimanawa Range (Lat. 40°S) near the most northern part of its distribution in New Zealand, in general it is most richly developed in low- to mid-altitude, ± open forest between 200 and 800 m where it often forms distinctive, large, shelf-like clones with the divergent, dichotomously branching lobes projecting from tree boles. It is an epiphyte of the following phorophytes: *Beilschmiedia tawa*, *Carpodetus serratus*, *Coprosma linearifolia*, *C. lucida*, *C. propinqua*, *Dacrydium biforme*, *D. cupressinum*, *Dacrycarpus dacrydioides*, *Dracophyllum longifolium*, *D. uniflorum*, *Griselinia littoralis*, *Hebe salicifolia*, *Hoheria glabrata*, *Fuchsia excorticata*, *Kunzea ericoides*, *Leptospermum scoparium*, *Libocedrus bidwillii*, *Melicytus ramiflorus*, *Metrosideros robusta*, *M.umbellata*, *Myrsine divaricata*, *Myrtus bullata*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *N. truncata*, *Olearia*, *Phyllocladus alpinus*, *Pittosporum tenuifolium*, *Podocarpus hallii*, *P. totara*, *Prumnopitys ferruginea*, *Pseudopanax crassifolius*, *Senecio eleagnifolius*, and *Weinmannia racemosa*.

In many habitats it is one of the major lichen epiphytes, frequently co-dominant with *Pseudocyphellaria multifida* and *Sticta subcaperata*, especially in mid-altitude forests west of the Main Divide in South Island. It is also a common component of the rich lichen assemblages found on tree bark in moderate to high light habitats, associating with the following lichens: *Coccotrema cucurbitula*, *Lobaria adscripta*, *Menegazzia pertransita*, *Metus conglomeratus*, *Nephroma australe*, *Pannaria immixta*, *Parmeliella nigrocincta*, *Phylctella sordida*, *P. subuncinata*, *Pseudocyphellaria colensoi*, *P. dissimilis*, *P. faveolata*, *P. glabra*, *P. homoeophylla*, *P. intricata*, *P. lividofusca*, *P. multifida*, *P. rubella*, *P. rufovirescens*, *Psoroma contextum*, *P. microphyllizans*, *P. pallidum*, *P. pholidotoides*, *P. sphinctrinum*, *Sphaerophorus melanocarpus*, *S. notatus*, *S. patagonicus*, *S. scrobiculatus*, *S. tener*, *Sticta filix*, *S. lacera*, *S. latifrons*, *S. subcaperata*, and *Usnea capillacea*.

Specimens examined: 130.

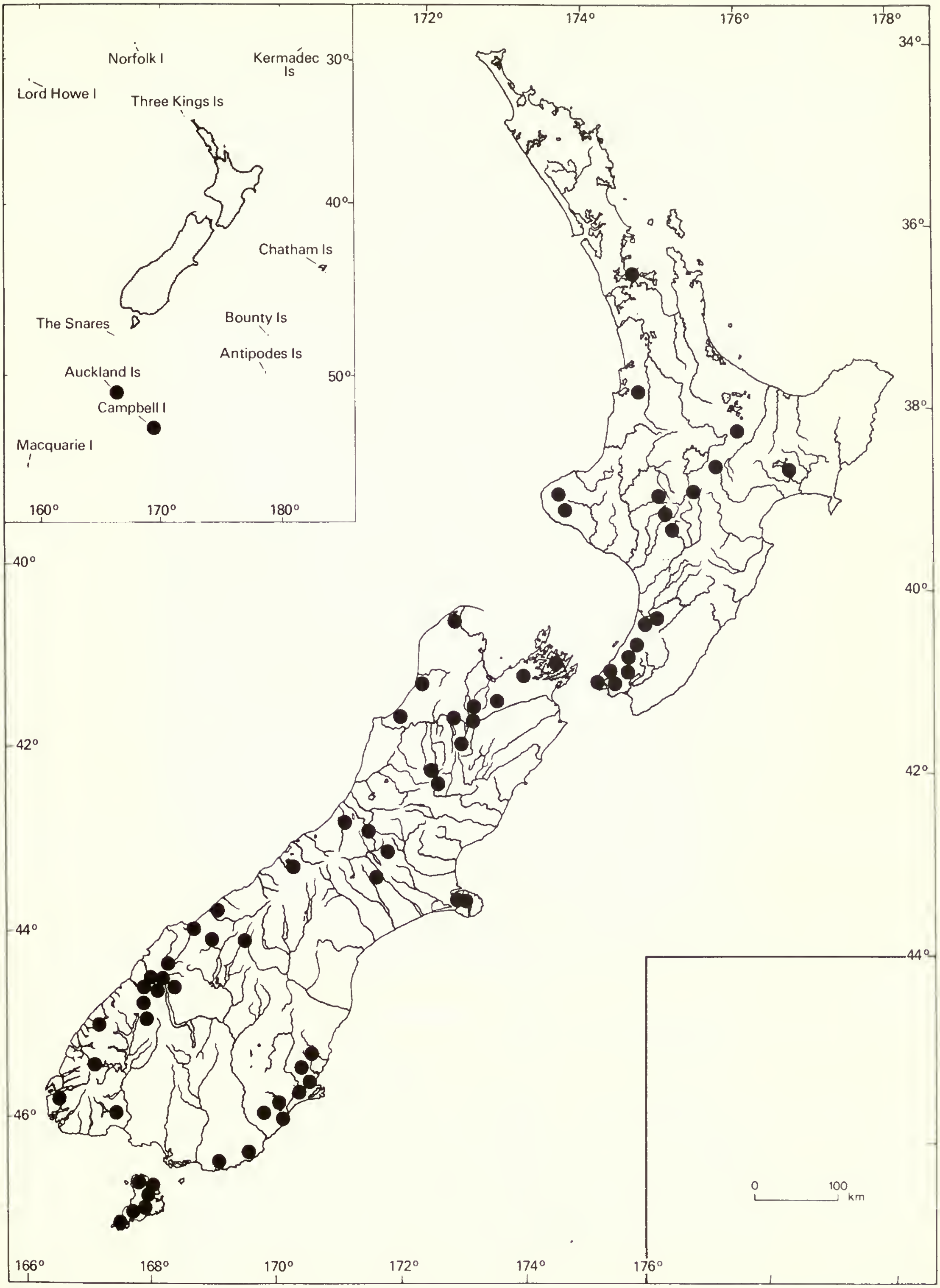
Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
50°
Auckland Is
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 27 Distribution of *Pseudocyphellaria billardierei*.

7. **Pseudocyphellaria carpoloma** (Delise) Vainio **Figs 28, 29**

in *Hedwigia* **37**: 34 (1898). – *Sticta carpoloma* Delise in *Mém. Soc. linn. Normandie* **2**: 159, pl. 19, right hand figure (1825). – *Stictina carpoloma* (Delise) Nyl., *Syn. meth. lich.* **1** (2) : 339 (1860). – *Saccardoa carpoloma* (Delise) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Cyanisticta carpoloma* (Delise) Gyelnik in *Feddes Reprium Spec. Nov. reg. veg.* **29**: 2 (1931). Type: New Zealand, 'Sur les vieux arbres à la Nouvelle Zélande', Bay of Islands, 1824, ?*R. P. Lesson* (PC-LENORMAND! – holotype) [see note 1].

Sticta impressa J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 648 (1844). – *Pseudocyphellaria impressa* (J. D. Hook. & Taylor) Vainio in *Hedwigia* **38**: 187 (1899). Type: New Zealand, sine loco (prob. Bay of Islands), *J. D. Hooker* (FH! – lectotype [fide Müller Argoviensis, (1888:13)]: BM! isotypes) [see note 2].

Sticta glaucolurida Nyl. in *Flora, Jena* **50**: 438 (1867). – *Lobaria glaucolurida* (Nyl.) Hellbom in *Bih. K.*

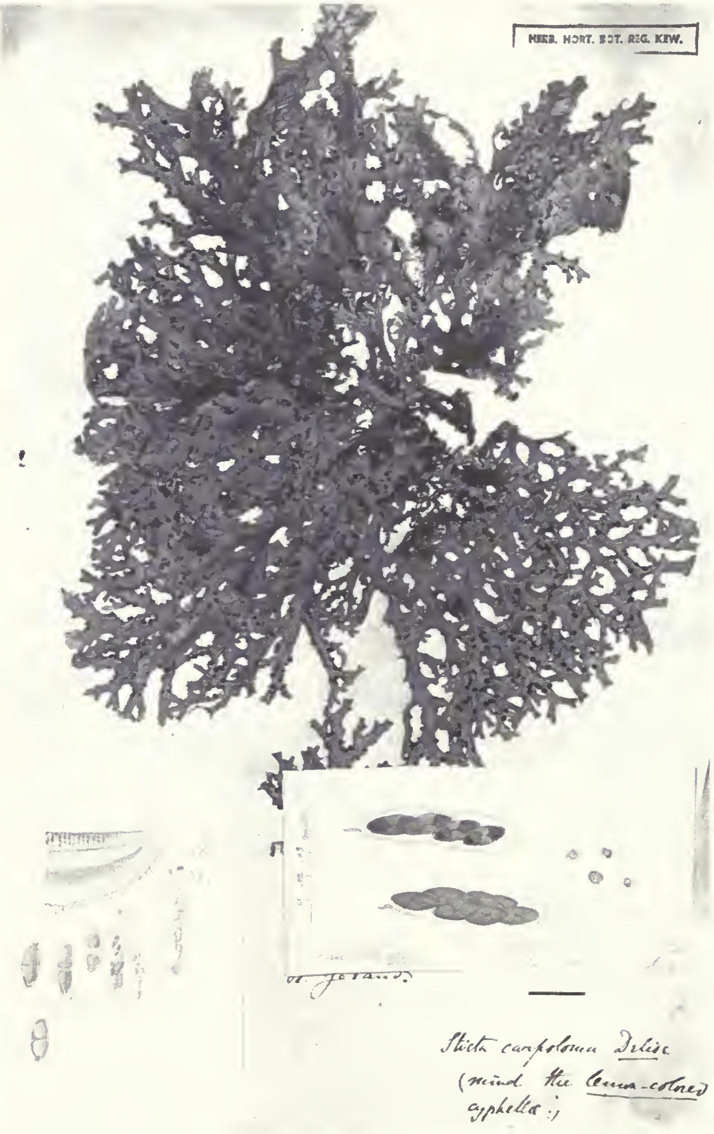

Fig. 28 *Pseudocyphellaria carpoloma*. New Zealand, *Hooker* (BM). Note Joseph Hooker's pencil sketches of anatomical details. Scale = 2 cm.

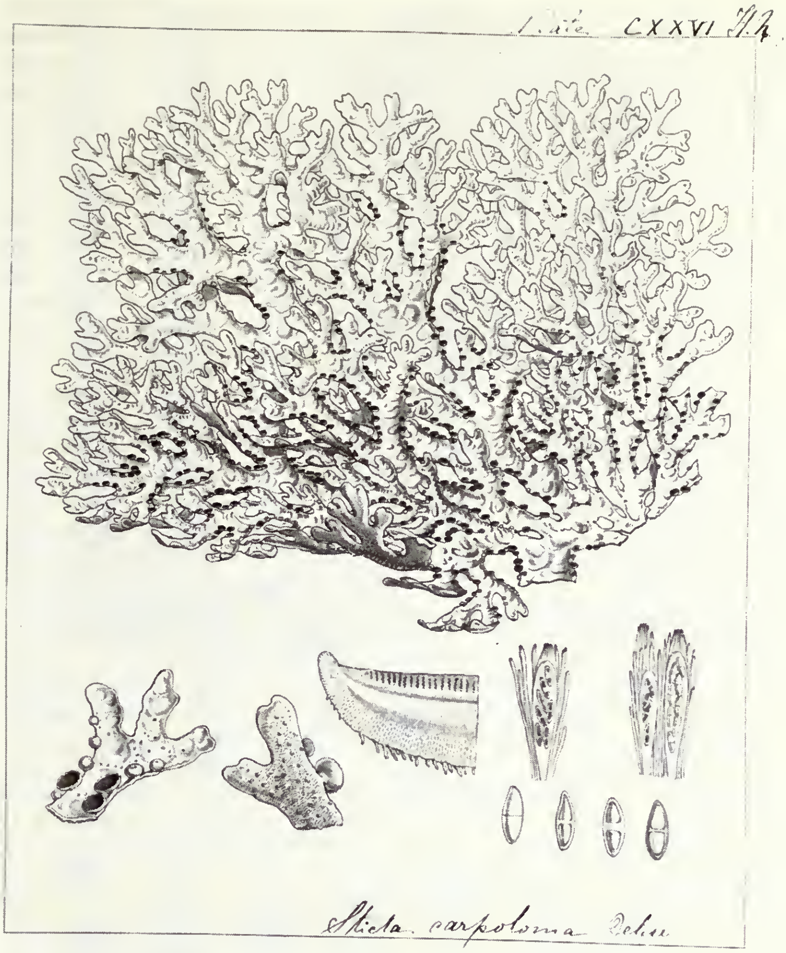

Fig. 29 W. H. Fitch's plate (of *Pseudocyphellaria carpoloma*) in *Flora Novae Zelandiae* based on specimen in Fig. 28. (BM).

svenska Vetensk. – Akad. Handl. **21** (3/13): 37 (1896). Type: Nova Zelandia, sine loco (prob. Wellington), 1867, *C. Knight* 10 (H-NYL 33587! – holotype). [see note 3].

Sticta borneti Müll. Arg. in *Flora, Jena* **65**: 204 (1882). Type: New Zealand, *D'Urville* (G! – holotype) [see note 4]. **Fig. 30**

Sticta expansa Stirton in *Trans. N. Z. Inst.* **32**: 72 (1900). Type: New Zealand, near Wellington, *J. Buchanan* (BM! – lectotype).

Note 1: *Sticta carpoloma* Delise
In 1980 the name *Sticta carpoloma* was lectotypified on material from Montagne's herbarium now in BM (Galloway & James, 1980:293); however, in 1982 Delise's original material was located in PC-LENORMAND (Galloway *et al.*, 1983*b*; Galloway & James, 1986). The holotype cited above represents material of this species from New Zealand that is named *S. carpoloma* in Delise's own handwriting (Galloway & James, 1986 fig. 5). A specimen in G! is annotated by Delise 'Sticta carpoloma D. Delise Stict. Specs de la Nouvelle Zélande (Donné a Delise par Bory de St-Vincent 1825)', and another in PC-HUE labelled by Delise 'Sticta carpoloma Delise', has the annotation '206 Baie des iles-Nouv. Zeelande. D. Lesson 1825'.

Sticta carpoloma is figured by Delise in plate 19 which is often missing from copies of the atlas illustrating his monograph on *Sticta*. In a copy of the atlas presented by Delise to the Linnean Society of London on 25 August 1828, both the plate number and the names of the two species depicted (*S. endochrysa* and *S.*

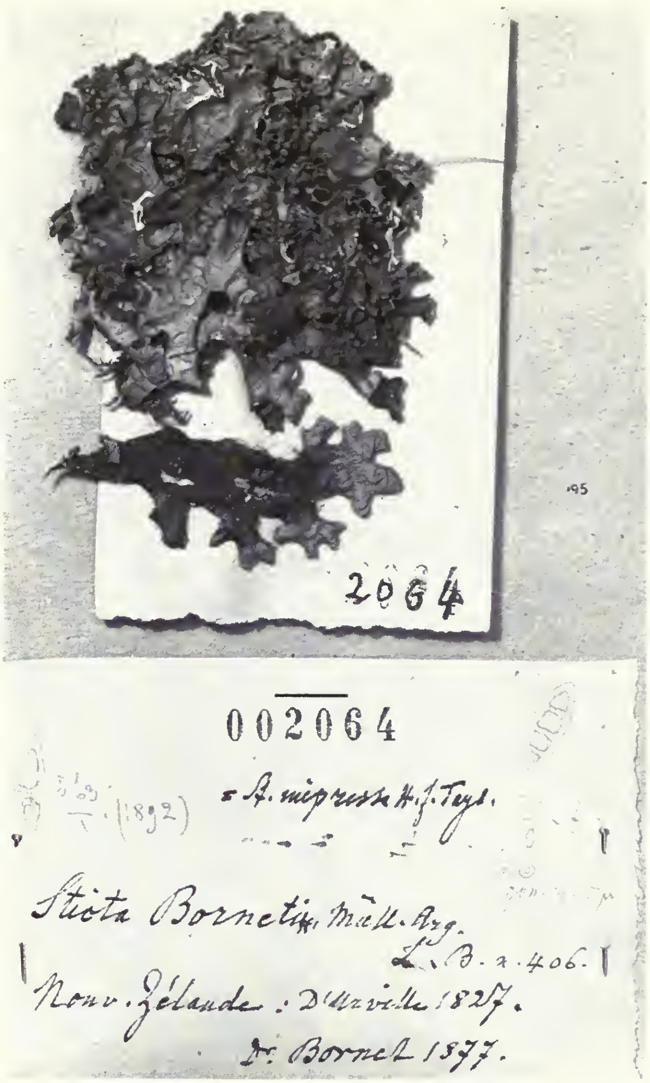
2064
002064
= S. impressa H. f. Tayl.
Sticta Bornetii, Müll. Arg.
L. B. 2. 406.
Nouv. Zélande : D'Urville 1827.
Dr. Bornet 1877.

Fig. 30 *Sticta borneti*. Holotype (G). Scale = 1 cm.

carpoloma) are marked on the page in Delise's hand (Galloway & James, 1986: fig. 5). *S. carpoloma* was collected in the Bay of Islands (North Auckland) in 1824. The corvette *Coquille*, captained by Louis-Isidore Duperrey anchored in the Bay of Islands from 3–17 April 1824 (Lesson, 1829, 1839) and both Lesson and D'Urville, botanists on the expedition, would have had opportunities to gather this conspicuous and usually well-developed lichen which is still prominent today in coastal vegetation in northern New Zealand. Bory de St-Vincent (1829: 236) records the species as Sticta corpoloma [sic] '6. Sticte corpolome, *Sticta corpoloma* Delise, Stict. suppl. (non figuré). M. Lesson a rapporté de nombreux échantillons de cette belle espèce, qui croît sur les vieux arbres autour de la Baie des Îles de la Nouvelle-Zélande', showing that although he was familiar with the description of the new species from New Zealand and had seen Lesson's collections of it, he was unaware of its having been engraved and figured in some copies of Delise's monograph.

After Delise's publication of *S. carpoloma*, the concept of the species changed in several accounts, introducing confusion to the correct circumscription of the taxon. Richard (1832) gave the name *S. carpoloma* to specimens of *Pseudocyphellaria rufovirescens* collected from Nelson, New Zealand (see Galloway *et al.*, 1983*b*: 140), ignoring the yellow pseudocyphellae alluded to in Delise's description as a good character for species separation. Hooker & Taylor (1844: 649) followed Richard's interpretation of *S. carpoloma*. Babington (1855: 276) gives a correct account of *S. carpoloma* and makes the following observations 'having exactly the habit of *S. foveolata* Del., from which it can scarcely be distinguished when the cyphellae are obsolete . . . In spite of a certain amount of variation in the length and breadth of the segments of the thallus, and of the more or less tomentose or quite naked under side, *S. carpoloma* is in general easily recognised by its deeply lacunose and forked lobes: the apothecia and medullary stratum agree with *S. crocata* . . . This plant does not bear soredia or coralline processes'. A fine coloured plate of a large specimen, complete with anatomical drawings of apothecia, hymenium, and spores (Plate CXXVI) accompanies Babington's account (see Fig. 29).

Both Nylander (1860*b*: 339–40) and Hue (1890: 297, 1901: 83–84) introduced further confusion when they recorded the photobiont of *S. carpoloma* as being blue-green, and the species also having soredia or isidia. Nylander recorded its range as being Chile, New Zealand, Tasmania, Polynesia, Java, and Réunion, to which Hue added Japan. Such a circumscription refers not to *P. carpoloma* sens. str., but to *P. desfontainii* (Delise) Vainio, and in part to *P. lechleri* and *P. gilva* from Chile.

Note 2: *Sticta impressa* J. D. Hook. & Taylor
Sticta impressa is one of a group of linear-laciniate, reticulate-faveolate species of *Pseudocyphellaria*, the protologue stating in addition 'sorediis [= pseudocyphellae] pallide flavis punctiformibus convexis apice impressis' (Hooker & Taylor, 1844: 648). Further, the species was reported by its authors as occurring in 'Lord Auckland's group, Campbell Island, Falkland Islands and New Zealand'. In choosing a lectotype of material labelled *S. impressa* by Thomas Taylor (such material exists in BM, FH, and M), Galloway & James (1980: 298) erroneously chose amply fertile material so labelled by Taylor from the Auckland Is having white pseudocyphellae and containing physciosporin. Consequently, *S. impressa* was judged to be *Pseudocyphellaria faveolata* and was accordingly incorporated in the synonymy of that species. However, such a procedure overlooks an earlier typification of *S. impressa* by Müller Argoviensis (1888: 137) who chose material from New Zealand (collected by Joseph Hooker) and present in Taylor's personal herbarium (FH). Müller Argoviensis (loc. cit) states of *S. impressa* 'simillima est *Stictae Billardieri* Del., sed pseudocyphellae definite sulphureo-flavae v. demum pallide flavae et minores, caeterum similiter hemispherico-v. conico-prominentes.' The type of *S. impressa* in Taylor's herbarium is annotated by Taylor 'Sticta impressa Tayl. sorediis flavis (Sticta carpoloma Hook. Herb.) (Sticta ochracea Tayl.) New Zealand, J. D. Hooker, 1844' (material collected at the Bay of Islands in 1841 by Hooker, was sent to Taylor in 1844). In Taylor's herbarium other material labelled *S. impressa* comes from New Zealand, collected by Dr Stanger, and by David Lyall (both are *P. carpoloma*); a specimen from New Zealand collected by Dr Stanger is referable to *P. billardieri* and one collected by Hooker from Campbell Island is *P. faveolata*. In Hooker's herbarium (BM) there are nine different specimens labelled *S. impressa* by Taylor; three are specimens of *P. faveolata* (J. D. Hooker collections from Auckland I., and from Campbell I., and a New Zealand collection of Dieffenbach), and six are of *P. carpoloma* (three collections of Hooker, one of Stanger, and one of Andrew Sinclair from Great Barrier I. One is without collector's name). A specimen of *P. gilva* (Ach.) Malme, collected by Lyall in the Falkland Is, is annotated *S. impressa* by Taylor (BM!). Of this Taylor wrote to Hooker 'S. impressa H.f & T. 'of Falklands' I happen not to have retained any such specimen – I suppose from New Zealand is not S. gilva Ach . . . S. ochracea Tayl. MSS I know to be S. carpoloma' (Taylor, Correspondence, Royal Botanic Gardens, Kew Director's Correspondence, **103** (98), 23 April, 1847).

Note 3: *Sticta glaucolurida* Nyl.
This taxon was lectotypified (Galloway & James, 1980: 293) on material collected by Knight and labelled by him (although not annotated by Nylander) *S. glaucolurida* Nyl., from Leighton's herbarium now in BM. Authentic material annotated by Nylander exists (H-NYL 33587) and consists of three minute scraps with three apothecia loose in the packet. Nylander (1867: 438–9) noted of *S. glaucolurida* 'prope *Stictam granulatam* in serie systematica locum habeat, sed affinis est *Stictae physciosporae*, a qua differt thallo sublaevi latius diviso et pseudocyphellis determinatae citrinis'.

Note 4: *Sticta borneti* Müll. Arg.
Type material of *Sticta borneti* (Fig. 30) is labelled by Müller Argoviensis as *S. impressa*, no doubt after 1882, for six years later Müller comments on New Zealand material of *P. carpoloma* (G 002600) under the name *Sticta impressa* (1888: 137). Müller Argoviensis (1894) lists *S. borneti* as a synonym of *S. impressa*, although he maintains *S. carpoloma* as a good species but following Nylander's interpretation has it with a blue-green photobiont in the genus *Stictina*.

Morphology: Thallus irregularly spreading, loosely entangled in often extensive festoons, corticolous, rarely saxicolous, 5–20(–50) cm diam. *Lobes* laciniate-elongate, plane to subconcave-subcanaliculate, discrete to entangled, ± dichotomously branching, 3–8 mm wide and 1–7 cm long, tapering from centre to periphery, apices blunt or pointed, often furcate, or ± shallowly notched or crenate. *Margins* entire, thickened below, with sparse to frequent, verruciform, conical, yellow pseudocyphellae projecting, decorticate area strongly to weakly pigmented. *Upper surface* bright lettuce green to olive green when wet, suffused brownish in parts especially towards apices of lobes, pale greyish green, buff or glaucous-brownish, suffused red-brown on storage in herbarium; strongly to obscurely faveolate, ridges rather smooth, faveolae deep to shallow and somewhat inapparent, matt, smooth, isidia, phyllidia, maculae, pseudocyphellae, and soredia absent, though in insect damaged specimens small irregular regenerating lobules can develop at margins and from edges of damaged lamina. *Medulla* white. *Photobiont* green. *Lower surface* pale whitish or yellowish at margins, buff, brownish to dark red-brown or ± blackened centrally, margins with a conspicuously and ± continuously raised rim, wrinkled, bullate, glabrous to sparsely or densely tomentose, tomentum pale, silky at margins, brown or black at centre. *Pseudocyphellae* scattered, very small. 0·1 mm diam. or less, on ridges, ± verruciform, decorticate area flat, yellow, conspicuous. *Apothecia* marginal or submarginal, subpedicellate, narrowly attached centrally, 0·5–3 mm diam., round to irregular to somewhat compressed, disc matt, pale to dark red-brown when wet, black when dry, imperforate, epruinose, exciple pale flesh pink or whitish, pubescent at first, then roughened-verrucose to ± scabrid, margins conspicuously dentate-striate often obscuring disc. *Pycnidia* sparse to frequent, on upper surface, small hemispherical swellings 0·5 mm diam. or less, apical pore minute, red-brown or black, surrounded by a pale marginal zone.

Anatomy: Thallus 120–200 μm thick (to 350 μm at margins). *Upper cortex* 25–30(–32) μm thick, dilute red-brown or yellow-brown in outermost 11–15 μm, zone abutting photobiont layer colourless, outer 2–4 μm of cells ± necrotic, pigment dissolving in K, cells 4·5–7 μm diam. *Photobiont layer* 18–22 μm thick, densely compacted, *photobiont* green ?*Dictyochloropsis*, cells rounded 2·5–3·5 μm diam. *Medulla* 50–75(–90) μm thick, appearing grey-black and ± granular in optical section (colour not changed in K), of loosely interwoven hyphae, to 4·5 μm diam., encrusted with crystals. *Pycnidia* oval or rounded, 180 μm diam. to 330 × 230 μm. *Lower cortex* 18–23 μm thick, lower 9–11 μm pale yellow-brown, inner 9–12 μm colourless, cells, 5–7 μm diam. *Tomental* hairs septate, simple, to 5 μm thick, in fascicles, (50–)65–140(–210) μm long, often with spores entangled at apices. *Apothecia: Exciple* without photobiont, of colourless, ± isodiametric, thick-walled cells arranged in parallel, radiating rows from centre to periphery, in basal parts cell rows elongating to form short tomental hairs, cells round to irregular 4·5–9 μm diam., walls to 2·5 μm thick, tissue 25–45 μm thick at margins, 70–100 μm thick near pedicel, sometimes formed into coarsely irregular clumps (scabrosity visible in × 10 lens) *Hypothecium* dilute yellow-brown, opaque, 45–65 μm thick. *Hymenium* 80–90(–100) μm tall, colourless; *epithecium* pale red-brown or yellow-brown, 6·5–11·5 μm thick paler in K. *Asci* cylindrical to clavate, 70–78(–85) × 12–16 μm. *Ascospores* grey-brown, oval-ellipsoid, thickened 1-septate, septum 4·5–7 μm thick, at maturity 3-septate (20–)22–25(–27) × 7–11 μm.

Chemistry: Methyl evernate, tenuiorin, methyl lecanorate, methyl gyrophorate, evernic acid (tr.), gyrophoric acid (tr.), hopane-7β, 22-diol, hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α, acetoxyhopane-7β, 22-diol (tr.), norstictic acid (tr.), stictic acid, cryptostictic acid, constictic acid, pulvinic dilactone, pulvinic acid, calycin, and several unidentified compounds.

Distinguishing features: Pseudocyphellaria carpoloma is one of a group of dichotomously branching, ± faveolate species well-developed in New Zealand. It has a white medulla, green photobiont, and prominent yellow pseudocyphellae on the lower surface and projecting from the margins. It has a distinctive chemistry [Code D of Wilkins & James (1979)].

Variation: In northern coastal forest where *P. carpoloma* is most commonly collected, individuals are characteristically ± narrow-lobed with branching of lobes, at least at the margins, dichotomous or subdichotomous, the whole thallus being somewhat open or loosely entangled. In southern populations (from Banks Peninsula and South Westland) lobes are much wider (1–2 cm wide in older, central parts) and much less obviously dichotomously branching, although the apical lobes are furcate to subdichotomously branched.

Occasionally, a distinctive closely attached rosette-forming ecotype of *P. carpoloma* is collected in which the lobes are attenuated and of ± equivalent length and breadth spreading into rosettes 10–15 cm diam. In this form individual lobes are hard to distinguish except at the margins which are sinuous-crenate and ± ascending and commonly also densely covered in small squamiform-dentate phyllidia which seem not to be developed as a response to injury, but rather to be induced by a particular microclimate and microhabitat. Such rosette forms are often also densely fertile, and may have a distinctive white pruinosity developed on the apices of some lobes. However, in all other respects (anatomically and chemically) the more compact, rosette-forming ecotype is exactly similar to the normal dichotomously branching form of *P. carpoloma*. An analogous situation exists in populations of *P. faveolata* (see below) with the compact, rosette-forming ecotype formerly being designated as *P. condensata*. Separate species designations for such ecotypes are not regarded as being either appropriate or necessary.

The particular combination of chemistry [Code D of Wilkins & James (1979)] and yellow pseudocyphellae distinguishes *P. carpoloma* from *P. faveolata* [Code B of Wilkins & James (1979), white pseudocyphellae, and apothecial discs which are white-pruinose at first and which lack a scabrid exciple], from *P. rufovirescens* [Code A of Wilkins & James (1979), white, punctate pseudocyphellae on a ± glabrous lower surface, and pale red-brown, epruinose apothecial discs], and from *P. billardierei* [Code C of Wilkins & James (1979), white pseudocyphellae (not present at the lobe margins)]. *P. physciospora* is distinguished from *P. carpoloma* by the entire margins which lack pseudocyphellae, the broader, and somewhat thinner lobes, and by differences in chemistry (most notably the production of appreciable amounts of norstictic and salazinic acids). See also Table 2 (p. 216).

Distribution: (Fig. 31) From the Three Kings Is (lat. 34°S) southwards in mainly coastal habitats from North Auckland to Kapiti I., in North I., and from Karamea Bluff (Nelson) to Milford Sound west of the Main Divide, and Arthur's Pass, Banks Peninsula and Taieri Mouth east of the Main Divide in South I. It occurs also on the Chatham Is. It has an altitudinal range from sea level to 300 m. Known from the following offshore islands: Three Kings Is, Cavalli Is, Poor Knights Is, Hen and Chickens Is, Little Barrier I., Great Barrier I., Rakitu I., Cuvier I., Rangitoto I., Kapiti I., and Chatham Is.

Habitat ecology: *Pseudocyphellaria carpoloma* is a common epiphyte on both bark and canopy twigs of the following photophytes in northern coastal forest: *Avicennia marina* var. *resinifera*, *Beilschmiedia taraire*, *Cordyline australis*, *C. kaspar*, *Dysoxylum spectabile*, *Elaeocarpus dentatus*, *Griselinia lucida*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *M. robusta*, *Pittosporum eugenioides*, *Planchonella costata*, *Podocarpus totara*, *Rhopalostylis sapida*, *Vitex lucens*, and *Weinmannia racemosa*. In South I. localities it grows on *Nothofagus solandri* var. *cliffortioides* and *Podocarpus hallii*. It has also been collected from basalt boulders under *Metrosideros excelsa*, from andesite boulders, and from rocks in open-canopied coastal forest. It favours similar ecological conditions to those in which *P. aurata* flourishes, and associates with the same group of lichens in these habitats (see under *P. aurata*).

Specimens examined: 105.

Exsiccatae seen: Arnold (1894) *Lichenes exsiccati* 1199 [As *Sticta glaucolurida* Nyl., Neuseeland, Knight (1886)]; Zahlbruckner & Redinger (1936) *Lichenes Rariores Exsiccati* 371. [As *Sticta impressa* Tayl. – Nova Zelandia: Ins. septentrionalis, in montibus Tararua, ad corticem *Nothofagi cliffortioidis* et *Weinmanniae racemosae*. Leg. H. H. Allan]. Material of this exsiccata was used by Magnusson (1940: 28–30) in his account of *P. carpoloma*.

8. **Pseudocyphellaria chloroleuca** (J. D. Hook. & Taylor) Du Rietz **Figs 32, 33**

in *Bot. Notiser* **1924**: 53 (1924). – *Sticta chloroleuca* J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 649 (1844). – *Pseudocyphellaria freycinetii* var. *chloroleuca* (J. D. Hook. & Taylor) Vainio in *Hedwigia* **38**: 187 (1899). – *Sticta freycinetii* var. *chloroleuca* (J. D. Hook. & Taylor) Zahlbr. in *Bih. K. svenska*

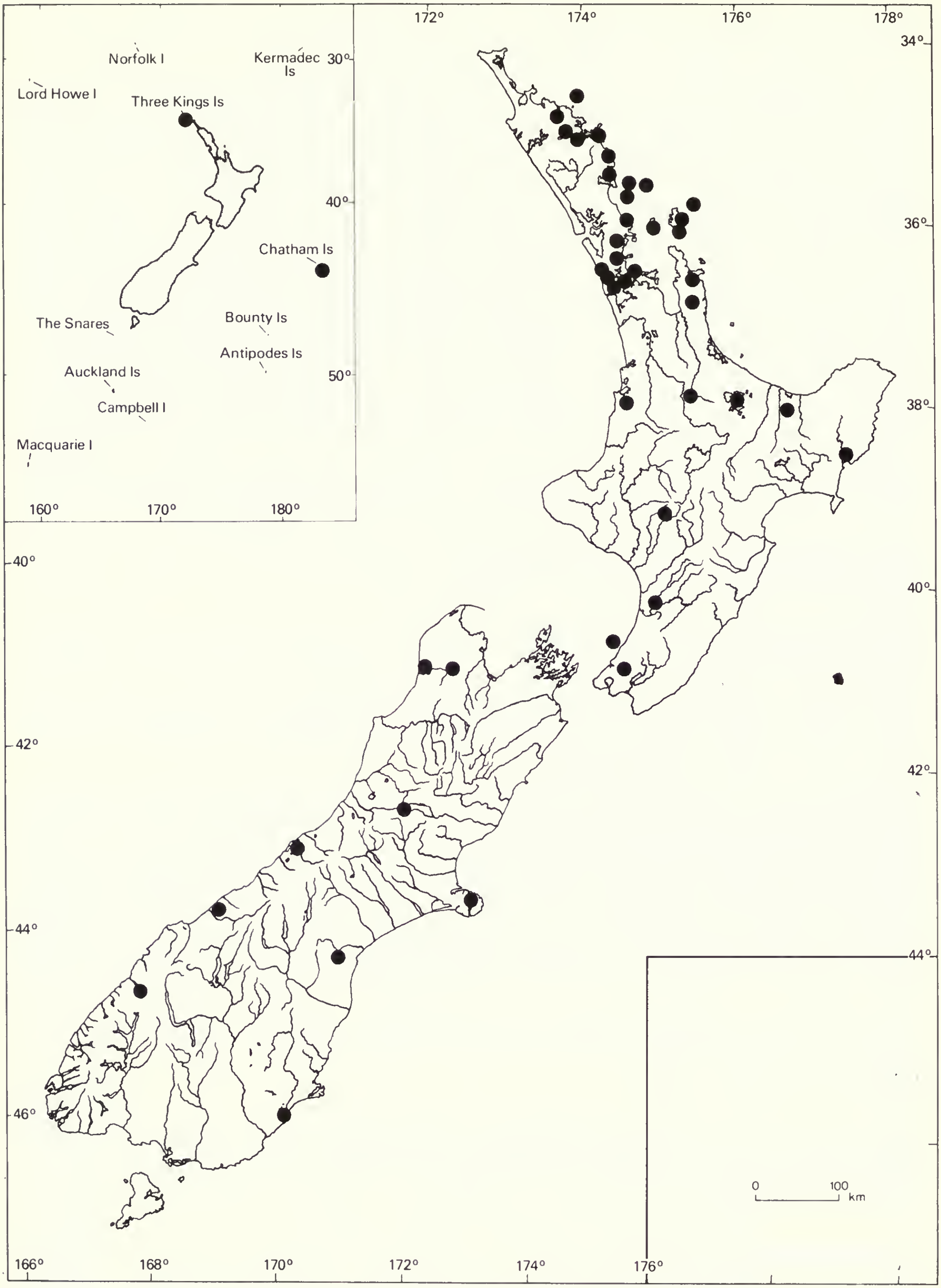
Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
50°
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0 100 km

Fig. 31 Distribution of *Pseudocyphellaria carpoloma*.

Vetensk. – Akad. Handl. **57** (6): 18 (1917). Type: New Zealand, sine loco, No 2 ho, *J. D. Hooker* (FH! – holotype; HM! – isotype) [see note 1].

Sticta psilophylla Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31**: 29 (1892). – *Pseudocyphellaria psilophylla* (Müll. Arg.) D. Galloway & P. James in *Lichenologist* **12**: 301 (1980). Type: New Zealand, sine loco, *C. Knight* (G! – holotype).

Sticta variabilis var. *cinerata* Zahlbr. in *Denkschr. Akad. Wiss. Wien math. – naturwiss. Kl.* **104**: 288 (1941). Type: New Zealand, North Island, Northland, Anawhata, in open *Leptospermum* shrubland on *L. scoparium* at *c.* 120 m, March 1935, *H. H. Allan* ZA 513 (W! – lectotype).

Note 1: *Pseudocyphellaria chloroleuca* (J. D. Hook. & Taylor) Du Rietz
When Du Rietz combined *Sticta chloroleuca* J. D. Hook. & Taylor in *Pseudocyphellaria*, he did so without having seen type material annotated by Taylor, and instead referred to material collected in New Zealand by Berggren, Helms, Jelinek and Knight, the isidiate austral species *P. glabra* (J. D. Hook. & Taylor) Dodge. Du Rietz (1924) correctly separated the isidiate *P. glabra* from the related non-isidiate *P. freycinetii*, but mistakenly placed *Sticta glabra* as a synonym of *S. chloroleuca*, with the result that for many years *P. glabra* was recorded in the literature as *P. chloroleuca*.

Galloway & James (1980) reinstated *P. delisea* (Delise) D. Galloway & P. James [*Sticta delisea* Delise is a superfluous name (see p. 149) and hence *Pseudocyphellaria delisea* becomes a synonym of *P. glabra*] as a good species [see also Hawksworth & Galloway (1984)] and included *P. chloroleuca* as a synonym, lectotypifying in error *Sticta chloroleuca* from New Zealand material collected and labelled by Joseph Hooker, but referable to *P. glabra* and not seen by Thomas Taylor who proposed the name *chloroleuca*. A recent examination of the holotype of *Sticta chloroleuca* from Taylor's herbarium (FH) shows this (Fig. 32) to be an independent Australasian species, quite distinct from *P. glabra*. The lectotypification of Galloway & James (1980: 297) must therefore be rejected (Art. 8) in favour of the holotype material annotated by Taylor. The taxon *P. psilophylla* (Müll. Arg.) D. Galloway & P. James, is a later name for *P. chloroleuca* and is reduced to synonymy with it (Galloway, 1986*b*).

Morphology: *Thallus* orbicular to irregular spreading, 5–20(–30) cm diam., corticolous, loosely attached centrally, margins and apices free. *Lobes* linear-elongate, very variable, 2–8(–12) mm wide, 1–4(–8) cm long, rarely to 15 cm long, apices discrete, complex-imbricate centrally, slightly convex to strongly canaliculate. *Margins* entire to ragged, lobulate-incised, sparsely to densely isidiate, slightly to strongly revolute, ascending. *Upper surface* bright lettuce green when moist, pale greenish grey often suffused red-brown towards apices when dry, becoming yellow-brown on storage, irregularly wrinkled to shallowly faveolate, matt, minutely scabrid-areolate (× 10 lens) in parts, also here and there minutely granular-papillate, isidiate, without soredia, maculae, phyllidia or pseudocyphellae. *Isidia* mainly marginal and there often densely developed, in small clumps laminally or originating from breaks and fissures, sometimes densely covering thallus in a thick crust, simple, fingerlike at first often in groups of 3–5, then branching and becoming coralloid, slender, fragile, 0·5–2 mm tall and 0·2 mm wide, terete or somewhat flattened, eroding and leaving small pits. *Medulla* white. *Photobiont* green. *Lower surface* white or pale buff-pink, glabrous, wrinkled-plicate to ± bullate, rarely very thinly and patchily white-tomentose centrally, distinctly ridged at margins. *Pseudocyphellae* white, minute, 0·1 mm diam. or less, numerous, inapparent, punctiform, flecklike, flat or slightly punctate. *Pycnidia* rare to occasional, marginal and on thallus ridges, minute, punctiform, red-brown, inapparent, not papillate. *Apothecia* sessile to subpedicellate, sparse to lacking, marginal and laminal, margins obscuring disc at first, excluded at maturity, 0·5–3·5 mm diam., cupuliform, concave at first becoming subconvex at maturity, disc pale yellow-brown to dark red-brown, matt to slightly glossy, epruinose, exciple white to pale flesh-coloured, translucent when moist, delicately scabrid-verrucose.

Anatomy: *Thallus* 120–180(–210) μm thick. *Upper cortex* 27–34 μm thick, upper 7 μm pale yellow-brown, remainder colourless, cells 7 μm to 9 μm diam. *Photobiont layer* 22–27(–34) μm thick, *photobiont* green, cells closely packed, to 7 μm diam. *Medulla* 65–160 μm thick, colourless, hyphae 2·5 μm thick. *Lower cortex* 15–20 μm thick, pale yellow-brown, cells 2–7 μm diam. *Apothecia: Exciple* colourless, 90–135 μm thick, cells 7–13·5(–18) μm diam, in irregular clusters towards margins. *Hypothecium* dilute yellow-brown to pale straw-yellow, 64–74 μm thick. *Thecium* 64–74 μm tall, colourless; *epithecium* 7–14 μm thick, pale yellow-brown, unchanged in K, tips of paraphyses overtopped by 4·5–9 μm of colourless, amorphous gel,

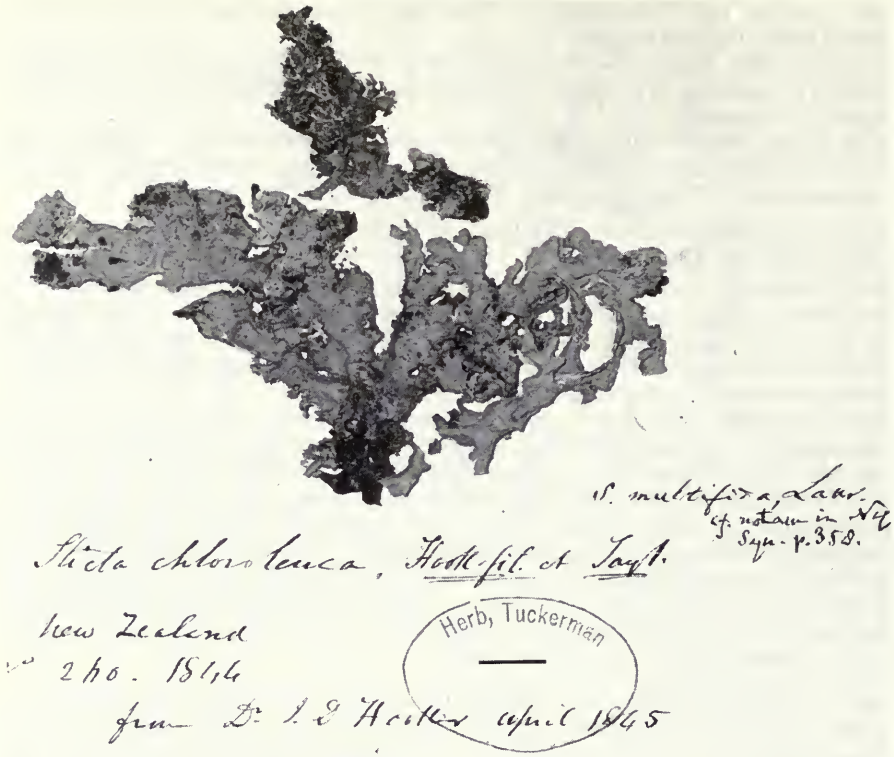
S. multifida, Laur.
cf. notam in N.Z. Syn. p. 358.
Sticta chloroleuca, Hook. fil. et Tayl.
New Zealand
No 260. 1844
from Dr. J. D. Hooker april 1845
Herb. Tuckerman

Fig. 32 *Sticta chloroleuca*. Lectotype (FH). Scale = 1 cm.

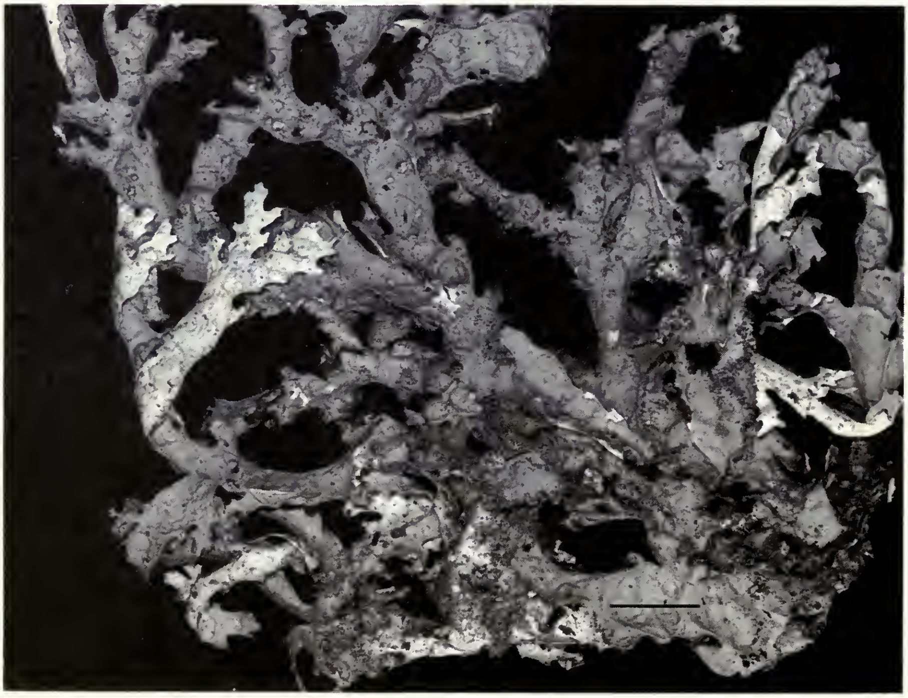

Fig. 33 *Pseudocyphellaria chloroleuca*. North of Westport, *Galloway* (BM). Scale = 2 cm.

paraphyses 2 µm diam., apices swollen, ± moniliform, upper 10–12 µm surrounded by a yellow-brown gel. *Asci* 78–83 × 13·5–15·5 µm. *Ascospores* brown, broadly ellipsoid-fusiform, apices rounded or pointed, 1-3-septate, 25–30 × 6·8–9·1 µm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol, methyl gyrophorate, and gyrophoric acid (C + red, often fugitive).

Distinguishing features: Pseudocyphellaria chloroleuca is an Australasian species characterized by its pale, glabrous lower surface, a white medulla, green photobiont, fragile, marginal and/or laminal, terete isidia (simple to coralloid), and a distinct but often fleeting C + red (gyrophoric acid) reaction of the cortex. The lobes are linear-elongate, often somewhat ragged, and convex to strongly canaliculate.

Variation: Pseudocyphellaria chloroleuca is a rather variable species, considerable differences in lobe width and length, and in manner of branching being encountered. Isidia are primarily marginal and at first are simple and finger-like, but later become coralloid-branched and somewhat flattened. Being rather fragile they are readily fractured or eroded, and leave small laminal pits which may be confused with pseudocyphellae. The pale, glabrous lower surface with inapparent, white pseudocyphellae, and the C + red cortical reaction readily distinguish *P. chloroleuca* from several other similar species which lack these characters (Table 1), viz. *P. glabra*, simple, terete isidia, a dark ± tomentose lower surface with prominent white pseudocyphellae, and a distinctive chemistry containing usnic acid and the stictic acid series of metabolites accompanying Code A hopanes; *P. corbettii*, as for *P. glabra* but with marginal and occasionally laminal, palmate phyllidia; *P. episticta*, laminal, white, scattered pseudocyphellae not derived from isidia, marginal to laminal, simple to coralloid-branched, phyllidia, and a ± tomentose lower surface, and with two hopane acids as medullary constituents; *P. fimbriata*, marginal phyllidia which are apically white-tomentose, thicker, more coriaceous lobes which are densely tomentose below; *P. wilkinsii*, as for *P. episticta*, but with two hopanes, and with fragile, terete, simple to coralloid isidia and marginal and laminal phyllidia.

Distribution: (Fig. 34) Three Kings Islands (lat. 34°6′S) to Wellington in North I., and Nelson to Westland (lat. 42°30′S) and Southland (lat. 46°30′S) in South I., mainly northern coastal, sea-level to 270 m. Also known from Lord Howe Island.

Table 1 Comparison of species similar to *Pseudocyphellaria chloroleuca*.

Character	*chloroleuca*	*corbettii*	*episticta*	*fimbriata*	*glabra*	*wilkinsii*
epithecium K + rose	−	−	+	−	−	−
Thallus isidiate	+	−	−	−	+	+
Thallus phyllidiate	−	+	+	+	−	+
Margins tomentose	−	−	−	+	−	−
Upper surface pseudocyphellate	−	−	+	−	−	+
Cortex C + red	+	−	−	−	−	−
Lower surface glabrous	+	−	−	−	−	−
Lower surface tomentose	−	+	+	+	+	+
15-acetoxy-22-hydroxyhopan-24-oic acid	−	−	+	−	−	−
15-22-dihydroxy-24-hopanoic acid	−	−	+	−	−	−
7-acetoxyhopan-22-ol	+	+	−	+	+	+
hopane-15α, 22-diol	+	+	−	+	+	+
Methyl gyrophorate	+	−	−	−	−	−
Gyrophoric acid	+	−	−	−	−	−
Stictic acid complex	−	+	−	−	+	−
Usnic acid	−	+	−	−	+	−

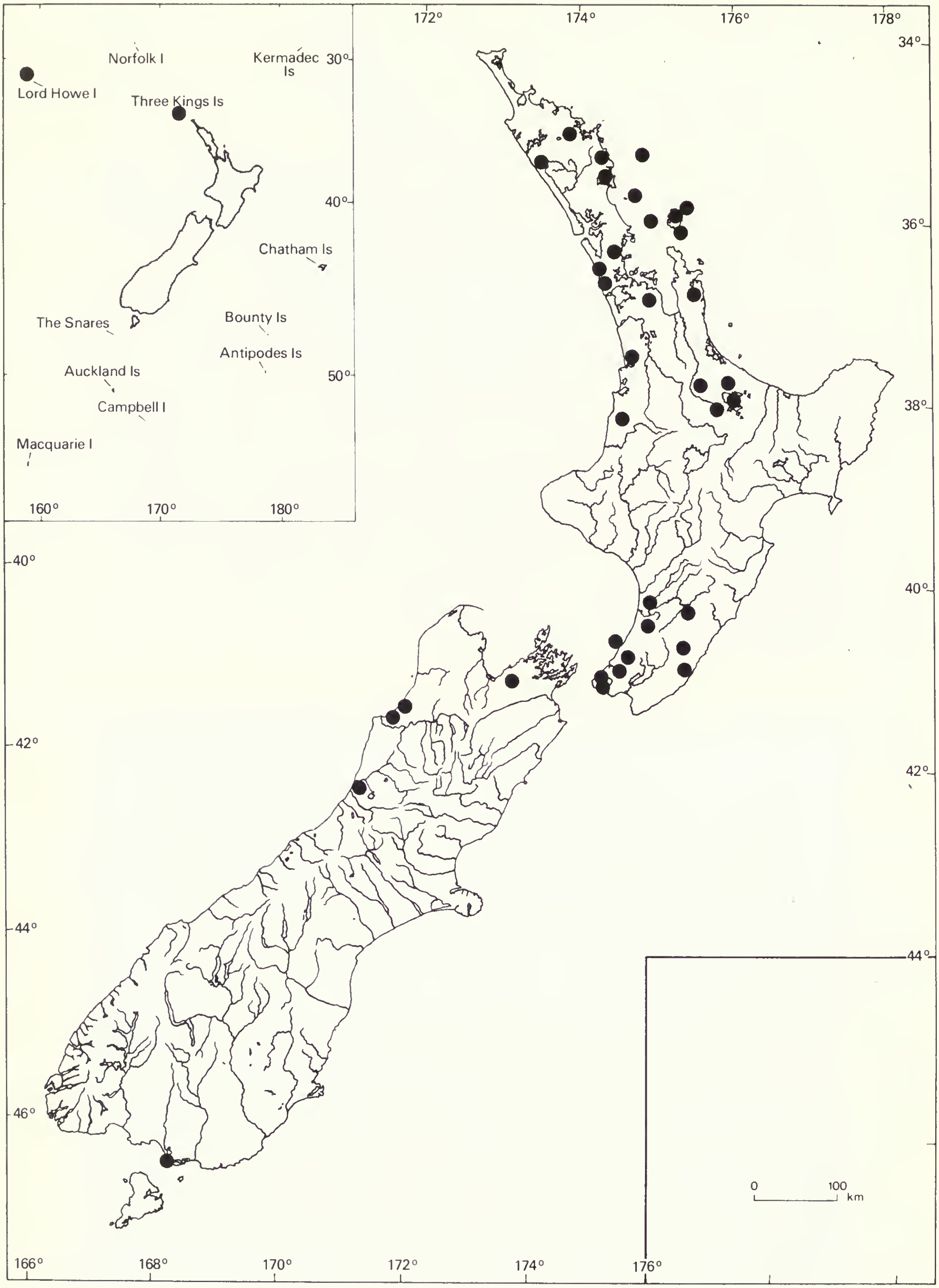
Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
40°
50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 34 Distribution of *Pseudocyphellaria chloroleuca*.

Habitat ecology: *Pseudocyphellaria chloroleuca* is a species of lowland, coastal forest and occurs in partially shaded habitats to dry, open situation in full sunlight. Although mainly epiphytic on trees or sbrubs, it is also occasionally found on rocks in partial shade. It is known from the following phorophytes: *Beilschmiedia tawa*, *Dacrycarpus dacrydioides*, *Elaeocarpus hookerianus*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *Myrsine australis*, *Phyllocladus trichomanoides*, *Rhipogonum scandens*, *Rhopalostylis sapida*, and *Weinmannia racemosa*. It is commonly associated in such habitats with the following lichens: *Pseudocyphellaria aurata*, *P. poculifera*, *P. wilkinsii*, *Sticta squamata*, *S. latifrons*, *Usnea arida*, and *U. rubicunda*.

Specimens examined: 55.

9. **Pseudocyphellaria cinnamomea** (A. Rich.) Vainio **Figs 35, 36**

in *Philipp. J. Sci. C.* **8**: 120 (1913). – *Sticta cinnamomea* A. Rich., *Voy. de l'Astrolabe*, *Bot.*: 28, tab. 8 fig. 3 (1832). Type: New Zealand. South Island, Nelson [Novae-Zelandiae, Havre de *l'Astrolabe*]. *D'Urville*, ex Herb. Bory de St-Vincent (PC-THURET! – holotype).

Sticta fragillima Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 279 (1855). – *Stictina fragillima* (Church.

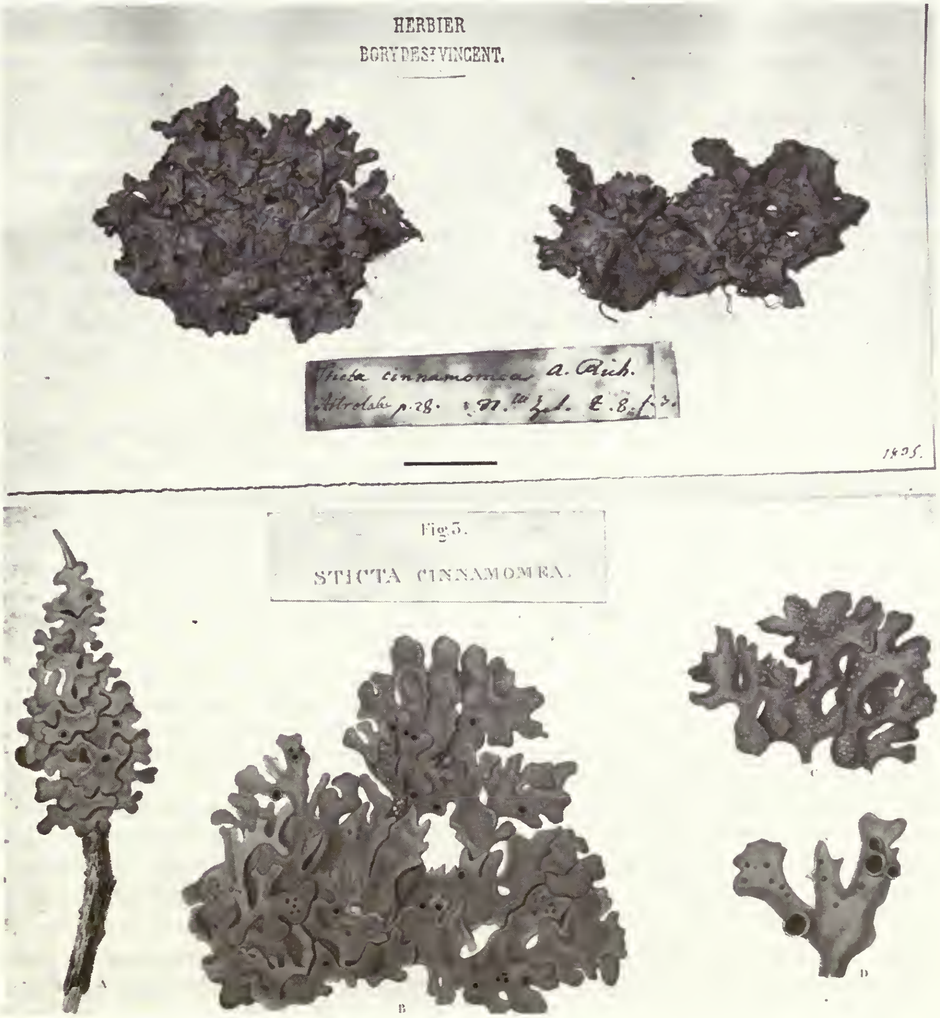
HERBIER
BORY DE ST VINCENT.
Sticta cinnamomea A. Rich.
Astrolabe p.28. N.lle Zel. t.8.f.3.
1835.
Fig. 3.
STICTA CINNAMOMEA.
A
B
C
D

Fig. 35 *Sticta cinnamomea*. Holotype (PC-THURET), and plate from Richard (1833). Scale = 1 cm.

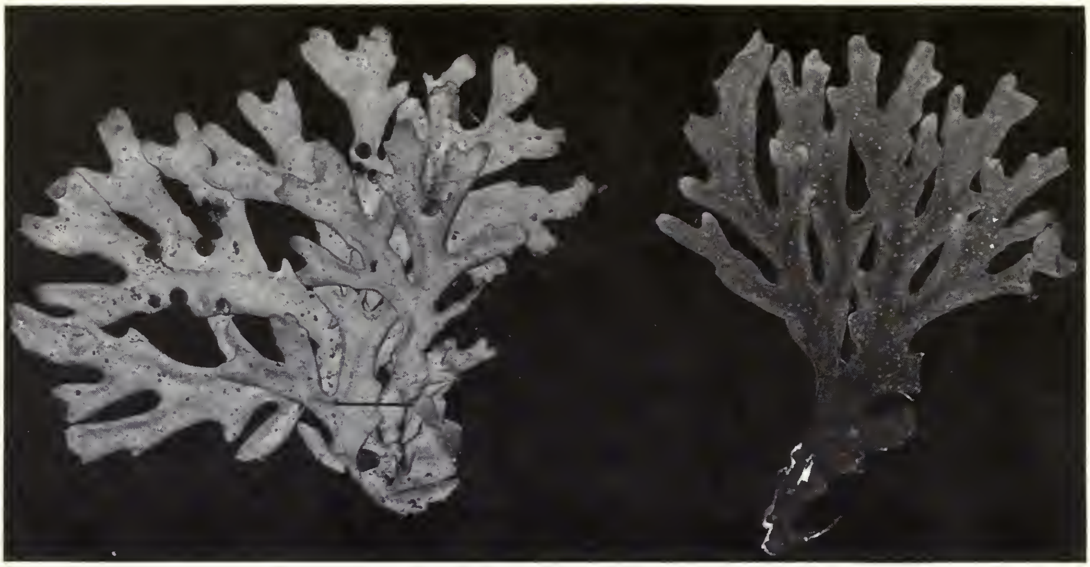

Fig. 36 *Pseudocyphellaria cinnamomea.* New Zealand, *J. D. Hooker* (NY). Scale = 1 cm.

Bab.) Nyl., *Syn. meth. lich.* **1**(2): 335 (1860). Type: New Zealand, sine loco, *J. D. Hooker* (BM! – lectotype) [see note 1].

Sticta fragillima var. *glaberrima* (Laurer) Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 279 (1855). Authentic material not seen.

Stictina fragillima f. *lutescens* Krempelh. *in* Nyl. in *J. Linn. Soc. Lond. Bot.* **9**: 246 (1866). – *Stictina fragillima* f. *sublutescens* (Krempelh.) Nyl. *in* Hue in *Nouv. Archs Mus. Hist. nat. Paris*, III, **2**: 296 (1890). – *Sticta fragillima* f. *lutescens* (Krempelh.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 30 (1896). Type: New Zealand, Nelson, Tarndale, *Dr A. Sinclair*, ex Herb. W. L. Lindsay (BM! – lectotype; BM!, E! – isotypes).

Icon: Krempelhuber 1870. Tab XIV. 2. [as *Sticta fragillima*].

Note 1: *Sticta fragillima* Church. Bab.
Babington (1855: 279) remarks of his *Sticta fragillima* and its variety β *glaberrima* 'Very similar to *S. damaecornis* in its ramification, and, like it, prone to considerable variation, as is apparent from the few specimens which I have examined. The consistency of the thallus, however, is widely different, and is so extremely brittle that most of the specimens are more or less mutilated. The central costa being more or less distinct, is likewise a character of importance. The var. β cannot be satisfactorily separated; the lobes are broader and shorter, and the colour is different; the under side likewise is sometimes, but not always, quite smooth . . . In all likelihood *S. cinnamomea* A. Rich. *Fl. de la N. Zel. p. 28. pl. 8, f. 3.* is a fine state of this form. It does not seem, however, to be costate; the apothecia are represented as very dark, and having a tolerably broad margin. I have seen no authentic specimens.'

In Babington's description of var. *glaberrima* which is based on Laurer's (1827) *Sticta glaberrima* (a tropical species of *Sticta* which has nothing whatever to do with *P. cinnamomea*), he mentions 'cyphellis urceolatis' which seems to refer to species of *Sticta*. However, there is no blue-green species of *Sticta* known from New Zealand remotely resembling *P. cinnamomea*, and it is likely that he confused ± marginate pseudocyphellae with true cyphellae.

Thomas Taylor annotated New Zealand specimens of *P. cinnamomea* collected by J. D. Hooker and by Dieffenbach with the unpublished name *Sticta digitata* Tayl. One Hooker specimen bears the following note in Taylor's hand 'Sticta digitata *n. sp.* this occurred in Dr Hooker's Collection. I know not how its character and description were omitted in the printing [obviously referring to the joint paper with Hooker, *Lichenes Antarctici* of 1844]. I shall send them again.'

Morphology: Thallus irregularly spreading, 5–10(–15) cm diam., corticolous, muscicolous, rarely terricolous, loosely attached centrally, margins and lobe apices free. *Lobes* linear-elongate, straplike, 2–6(–8) cm long, usually rather narrow, 2–5(–8) mm wide, rarely to 15 mm wide, subcanaliculate, irregularly to subdichotomously branching, often somewhat constricted at branch points, sinuses wide-angled. *Margins* entire, noticeably ridged below, very rarely secondarily lobulate or with scattered, white, punctiform pseudocyphellae. *Upper surface* dark slate blue or yellowish blue, often with white or buff blotches or spots (photobiont-free zones), pale grey to cinnamon-brown or yellowish when dry, plane, shallowly undulate to convex at apices, centrally shallowly canaliculate, not cracked or wrinkled, often minutely white- or buff-warty-papillate, smooth, matt or slightly glossy in parts, rather coriaceous, without soredia, isidia, phyllidia or pseudocyphellae. *Maculae* minute (use × 10 lens) best seen when moist. *Medulla* white. *Photobiont Nostoc. Lower surface* white to pale yellow-buff at margins, pale to dark brown centrally, short, velvety tomentose from margins to centre, or with a narrow, glabrous marginal zone, smooth to minutely wrinkled at margins, often with a prominent, slightly darkened, raised midrib. *Pseudocyphellae* white, sparse to numerous, scattered, minute, 0·05 to 0·2 mm diam., flecklike, very shallowly verruciform, margins slightly raised, apparent only in larger pseudocyphellae, decorticate area flat to concave. *Pycnidia* occasional to moderately common, scattered, laminal, often ± common towards lobe apices, shallowly papillate, to 0·2 mm diam., apical ostiole red-brown to black, punctate-depressed. *Apothecia* marginal, sparse or absent to occasional, sessile, constricted at base, 0·4–4 mm diam., rounded, concave at first, becoming plane to subconvex, disc pale to dark red-brown, smooth, matt, epruinose, exciple whitish to pale flesh-coloured, translucent when wet, minutely verrucose-areolate or ± granular, not tomentose, ± crenate at margins of disc.

Anatomy: Thallus 230–370 µm thick. *Upper cortex* 34–45 µm thick, outer 10–12 µm pale straw-yellow, remainder colourless, central row of cells to 14 µm diam, outer and inner rows of cells 4·5–6·5 µm diam. *Photobiont layer* 27–46 µm thick, *photobiont Nostoc* in irregular clusters, cells to 7 µm diam. *Medulla* 110–230 µm thick, hyphae to 6 µm diam. *Lower cortex* 34–40 µm thick, outermost cells pale straw-yellow, remainder colourless, cells adjoining medulla compressed, inner rows of cells 7–13·5 µm diam. Tomental hairs 7–9 µm diam., 45–275 µm long, single or in fascicles. *Apothecia: Exciple* 70–110(–140) µm thick. *Hypothecium* 45–55(–73) µm thick, dilute yellow-brown to ± hyaline, opaque, unchanged in K. *Thecium* 110–137 µm tall, colourless; *epithecium* 11·5–15 µm thick, pale to dark yellow-brown or olive-brown, slightly granular, unchanged in K. *Asci* 76–92 × 11·5–15·5 µm. *Ascospores* pale yellow-brown, fusiform-ellipsoid, 1-3-septate, apices rounded or pointed, straight or slightly curved, 25–32(–34) × 7–9 µm.

Chemistry: Gyrophoric acid (tr.), 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: Pseudocyphellaria cinnamomea is an Australasian species having linear-elongate, straplike, rather narrow lobes, which are subcanaliculate, ± subdichotomously branching, and with entire, non-isidiate margins. It has a white medulla, a blue-green photobiont, and the lower surface is distinctly costate. Apothecia occasional to rare or absent, marginal, sessile, exciple whitish, minutely verrucose-areolate. Spores pale yellow-brown, 1-3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)]. It is a papery, rather brittle species and in older parts gives the impression of being stalked. On prolonged storage, specimens stain herbarium paper reddish brown.

Variation: Pseudocyphellaria cinnamomea is a rather uniform species, well-developed specimens having wider (to 15 mm wide) lobes than the normal 2–5(–8 mm). It is closely related to *P. dissimilis* but is distinguished from it by the entire, non-isidiate margins and the canaliculate lobes having a well-defined midrib on the lower surface. *P. allanii* differs from *P. cinnamomea* in having thick, coriaceous, sometimes minutely areolate-scabrid lobes with tomentose margins and/or upper surface, and the densely tomentose lower surface which is non-costate. *Pseudocyphellaria insculpta*, an Australian taxon differs from *P. cinnamomea* is having richly divided to ± phyllidiate lobes, a punctate-impressed upper surface, and broader and longer spores (27–)29·5–34(–36) × 9–13·5 µm. *Pseudocyphellaria fimbriatoides* is distinguished from *P. cinnamomea* by its marginal, hirsute phyllidia; *P. murrayi* by its dichotomously branched, reticulate-faveolate lobes, with a pale sometimes ± glabrous lower surface and no midrib; and

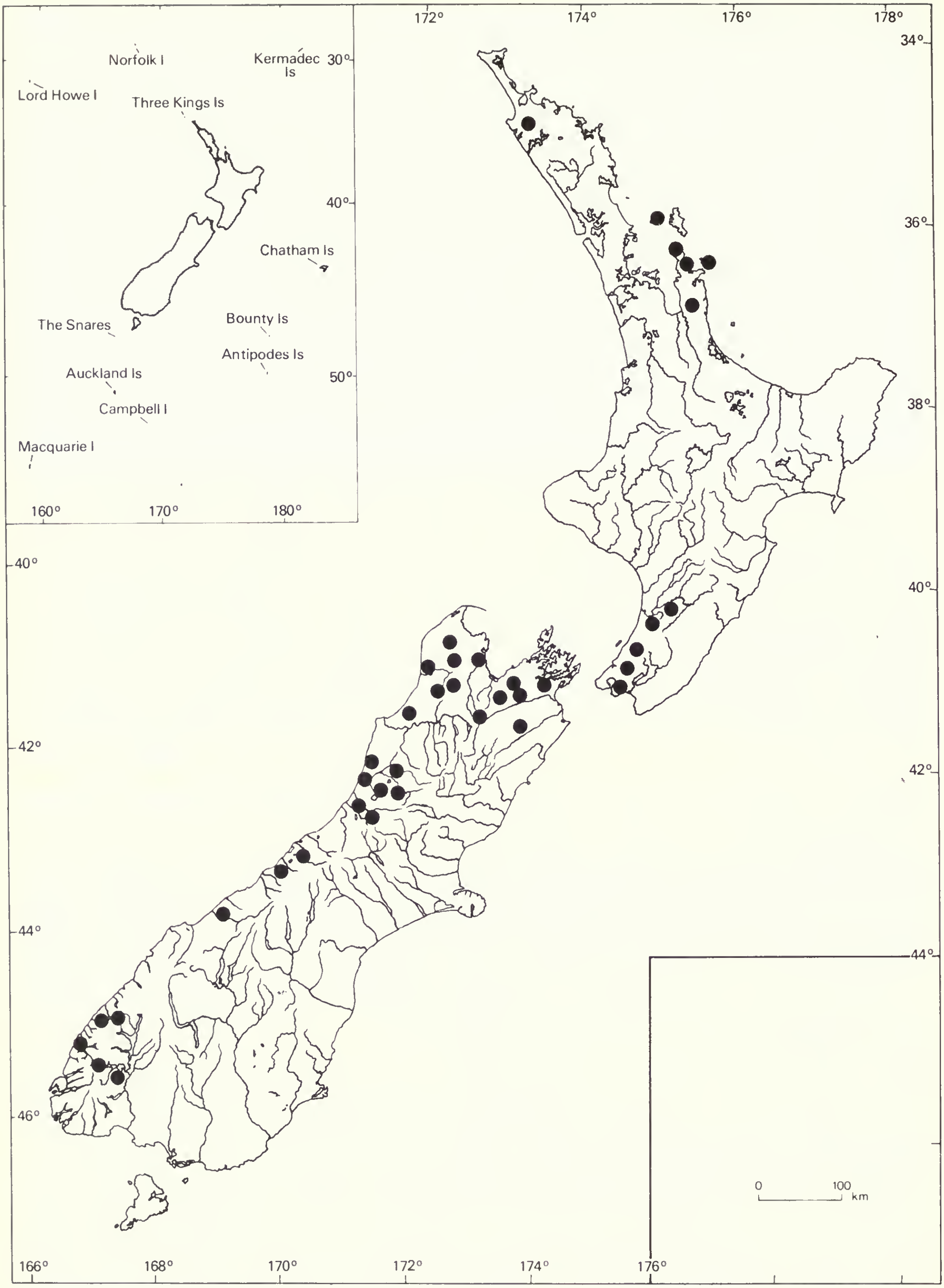
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Fig. 37 Distribution of *Pseudocyphellaria cinnamomea*.

P. junghuhniana, a widely distributed palaeotropical species, by the subdichotomously branching lobes which have a distinctive, dimpled, punctate-impressed upper surface.

Distribution: (Fig. 37) From North Auckland (lat. 35°S) to Wellington in North I., and from Nelson to Fiordland in South I., where it is most common west of the Main Divide; sea-level to 920 m.

Habitat ecology: Pseudocyphellaria cinnamomea is a species of deep shade, most commonly found on the bases of forest trees or shrubs, or on stones or boulders among mosses and ferns on the forest floor or even growing directly on soil. It is best developed in densely shaded, moist, humid habitats in high rainfall areas (it is especially rich in Westland and Fiordland), particularly on rocks alongside streams, or in waterfall spray. It is epiphytic on the following phorophytes in mainly lowland or coastal forest: *Beilschmiedia tawa*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Freycinetia baueriana* ssp. *banksii*, *Metrosideros excelsa*, *M. umbellata*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, and *Rhipogonum scandens*.

Specimens examined: 68.

10. Pseudocyphellaria colensoi (Church. Bab.) Vainio **Fig. 38**

in *Résult. Voy. S. Y. Belgica, Bot. Lich.*: 28 (1903). – *Sticta colensoi* Church. Bab. in J. D. Hook., *Fl. nov.–zel.* **2**: 274 (1855). – *Sticta urvillei* var. *colensoi* (Church. Bab.) Nyl., *Syn. meth. lich.* **1** (2): 360 (1860). – *Lobaria colensoi* (Church. Bab.) Trevisan, *Lichenotheca veneta* exs. 75 (1869). Type: New Zealand, sine loco, *J. D. Hooker* (BM! – lectotype) [see note 1].

Sticta colensoi var. *pinnatifida* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 274 (1855) Pl. CXXIII. *S. urvillei* f. *pinnatifida* (Church. Bab.) Stizenb. in *Flora, Jena* **81**: 177 (1895). – *Lobaria colensoi* f. *pinnatifida* (Church. Bab.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 41 (1896). Type: New Zealand, sine loco, *W. Colenso* (BM! – holotype) [see note 2].

Pseudocyphellaria neozelandica Dodge in *Nova Hedwigia* **19**: 468 (1971). Type: New Zealand, Canterbury, road to Arthurs Pass, on *Nothofagus*, *C. W. Dodge* 61-B10 (? FH – not seen).

Note 1: *Sticta colensoi* Church. Bab.
Babington (1855: 274) writes of this conspicuous plant 'A perplexing and variable species, but I do not see to what other it can be safely united: its nearest ally is perhaps *S. orygmaea* (Raoul's specimen is named *S. orygmaea*) [= *P. coronata*], but in *S. Colensoi* the thallus is usually thicker, less minutely scrobiculated, more divided, and differently coloured; the beautiful violet tint is wanting, though in decay the plant is sometimes obscurely blotched with purple; the under side is less brightly-coloured and more even; coral-like processes *yellowish* (rising from the gonimical stratum). The apothecia, however, perhaps afford the best marks, as above indicated'.

Note 2: *Sticta colensoi* var. *pinnatifida* Church. Bab.
This name refers to highly divided, ragged forms of *P. colensoi* which are common throughout the range of the species and without any taxonomic significance. A fine coloured engraving of this taxon (Pl. CXXIII) is given in Babington's account.

Morphology: Thallus orbicular to spreading, often ± pendulous, in irregular clustered clones, 8–20(–40) cm diam., corticolous, rarely saxicolous, loosely attached centrally, margins free, ascending. *Lobes* linear-elongate to somewhat broadly rounded, 10–25(–30) mm wide, 5–12(–15) cm long, irregularly incised or notched, discrete at margins to ± complex-imbricate centrally. *Margins* crenulate, notched, often torn or rather ragged, ± ascending to ± revolute, slightly thickened and often ± eroded and yellow or orange-red pseudocyphellate below, sparsely to densely isidiate. *Upper surface* bright lettuce green, yellow-green or tinged pale bluish green when moist, pale green-grey becoming ± tawny yellow or golden-brown when dry and on long storage, undulate, pitted, wrinkled-ridged or shallowly to deeply faveolate, often cracked or ± deeply fissured, matt or glossy, minutely scabrid in part (use × 10 lens), without soredia, maculae or pseudocyphellae, ± consistently isidiate. *Isidia* marginal and laminal, scattered in small random groups or erupting in clusters or lines on ridges and along breaks in thallus, minute, nodular or delicately fingerlike and fragile at first, soon becoming ± flattened, bifurcating to coralloid, inflated at apices, verruciform-granular, often densely clustered on

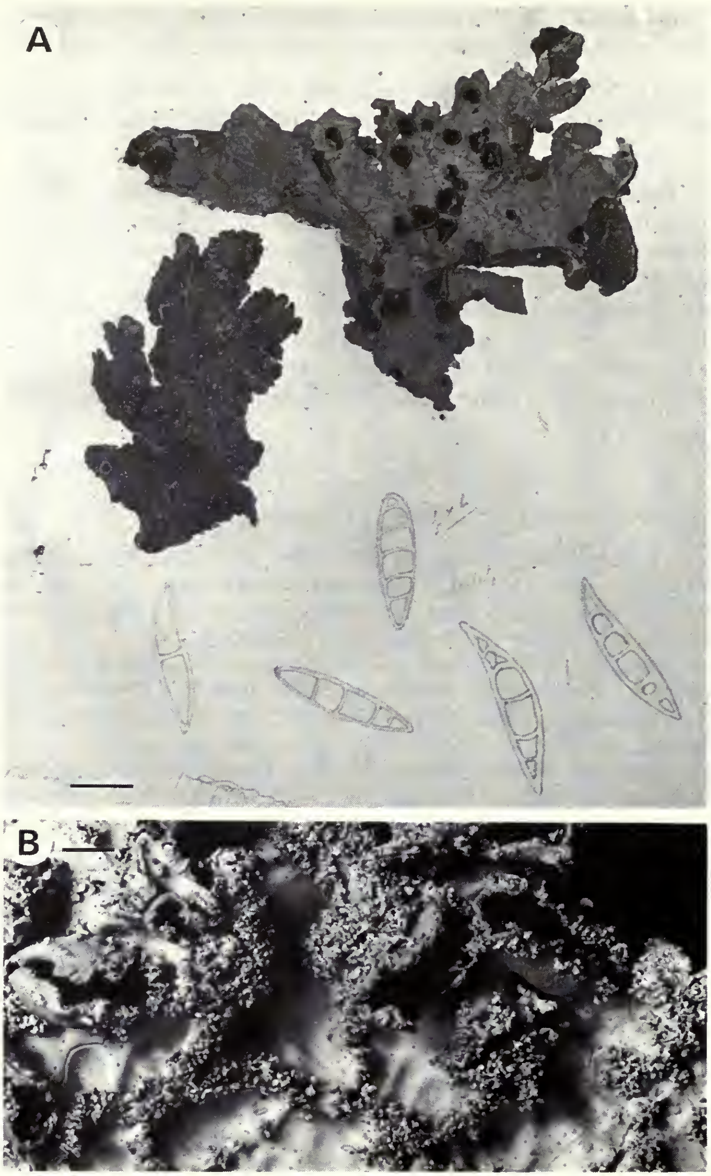

Fig. 38 *Pseudocyphellaria colensoi*. A. New Zealand, *Knight* (WELT). Scale = 1 cm. B. Lake Howden, *Scott* (COLO). Scale = 1 mm.

laminal ridges, at lobe margins or on apothecial exciple, often eroding apically and appearing yellow, normally concolorous with thallus, sometimes becoming dorsiventral with distinct upper and lower surface as in parent thallus. *Medulla* yellow, often appearing orange-red in thallus breaks or cracks. *Photobiont* green. *Lower surface* pale yellow, yellow-grey to tawny at margins, darkening to yellow-brown, red-brown to ± blackened centrally, thinly tomentose from margins to centre, tomentum short, uniform to ± scattered arachnoid in parts, pale buff to brownish, shallowly wrinkled to ± bullate. *Cephalodia* scattered in prominent, rounded warts, glabrous to ± tomentose, 1–2 mm diam. *Pseudocyphellae* conspicuous, numerous, rounded, on prominent verrucae raised above tomentum, 0·05–0·2(–0·3) mm diam., margins prominent, shining, brown to red-brown, opaque, decorticate area flat to convex, yellow. *Pycnidia* scattered, laminal or submarginal, punctiform, 0·1 mm diam., ostiole red-brown to black, often moribund and excavate, appearing as small, scattered pinholes in rows or clusters. *Apothecia* rare to numerous, pedicellate, submarginal or laminal, rounded, (1–)2–10 mm diam., often contorted through mutual pressure, disc pale to dark red-brown or orange-brown, matt, epruinose, margins sparsely to densely isidiate often also ± eroded and appearing yellow to orange-red, exciple concolorous with thallus or slightly paler, sometimes appearing pale flesh-coloured, conspicuously scabrid-areolate, often ± eroded-isidiate in well-developed specimens and appearing yellow-pseudocyphellate.

Anatomy: Thallus 250–410(–540) μm thick. *Upper cortex* uneven, 45–68 μm thick, upper 10–18 μm pale yellow-brown, remainder colourless, of thick-walled cells 1·5–3 μm diam. *Photobiont layer* 20–45 μm thick, *photobiont* green, cells rounded, closely packed 3–7 μm diam. *Medulla* 155–300(–450) μm thick, of loosely to compactly interwoven hyphae 4·5 μm diam., two dense bands 90 μm thick (200 μm thick at pseudocyphellae) of hyphae encrusted with dark red-brown crystals immediately below photobiont layer and above lower cortex. *Lower cortex* 27–35 μm thick, layer (8–10 μm) close to medulla pale yellow-brown, remainder colourless, of thick-walled cells 1·5–3 μm diam. *Tomental hairs* 5–7 μm thick, 25–185 μm long, pale yellow-brown, in fascicles. *Apothecia:Exciple* 100 μm thick at margins, 135–200 μm thick below disc, splitting away in ragged, pyramidal clusters (scabrosity), cells 4·5–9(–11) μm diam., thick-walled. *Hypothecium* 45–65 μm thick, hyaline to pale straw-yellow or yellow-brown, opaque, appearing slightly granular. *Thecium* 105–155 μm tall, colourless; *epithecium* 11–16 μm thick, dilute yellow-brown, unchanged in K; *paraphyses* colourless to pale straw-yellow, apices swollen, not moniliform. *Asci* 60–100 × 15–18 μm. *Ascospores* hyaline to pale yellow-brown, 1-3-septate, oval-ellipsoid or broadly fusiform, apices pointed, straight or slightly curved, (27–)32–36·5(–41) × 9–11 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, polyporic acid, 2α, 3β, 22α-triacetoxystictane, 22α-hydroxystictane-3-one, 2α, 3β-diacetoxystictane-22-ol, stictane-3β, 22α-diol, 2α-acetoxystictane-3β, 22α-diol, 3β-acetoxystictane-2α, 22α-diol, stictane-2α, 3β, 22α-triol.

Distinguishing characters: Pseudocyphellaria colensoi is a large, conspicuous Australasian species having linear-elongate to broadly rounded lobes, with irregular notched, ± ragged, and often deeply incised margins. The upper surface is undulate, pitted to ± reticulate-faveolate, with marginal and laminal isidia scattered in groups or arranged in lines on ridges or along thallus breaks. Isidia ± flattened, bifurcate to coralloid, verruciform-granular, often abraded apically and appearing yellow. It has a yellow medulla, a green photobiont, and a wrinkled to ± bullate, thinly tomentose lower surface. Apothecia are common (often numerous), large, to 1 cm diam., pedicellate, with eroded-isidiate margins. Spores are colourless to pale yellow-brown, 1-3-septate. The chemistry is dominated by stictanes (Chin *et al.*, 1973) and the acetone extract is yellow.

Variation: The major morphological variation seen in this species is in the size of the lobes which may vary from 1–3 cm wide, and from 5–15 cm long. All other characters are ± constant, although some variation is seen in the numbers of isidia and/or apothecia. *P. colensoi* is most closely related to *P. coronata*; however, *P. coronata* differs in having broadly rounded, not ragged-indented lobes, numerous, scattered, semi-immersed to sessile apothecia with dentate-coronate margins, and a characteristic red-magenta extract in organic solvents.

Distribution: (Fig. 39) From Rangitoto I., (lat. 36°45′S) to Cook Strait in North I., and from Nelson to Southland in South I., also in Stewart I., coastal and inland, lowland to subalpine, sea-level to 1500 m.

Habitat ecology: Pseudocyphellaria colensoi is an epiphyte of trees and shrubs in a variety of habitats, e.g. northern coastal forest, lowland podocarp-hardwood forest, upland *Nothofagus* forest, *Leptospermum* scrub, and lowland to subalpine scrub. Although most luxuriantly developed on tree boles, it also colonizes twigs and small branches. It prefers medium to high

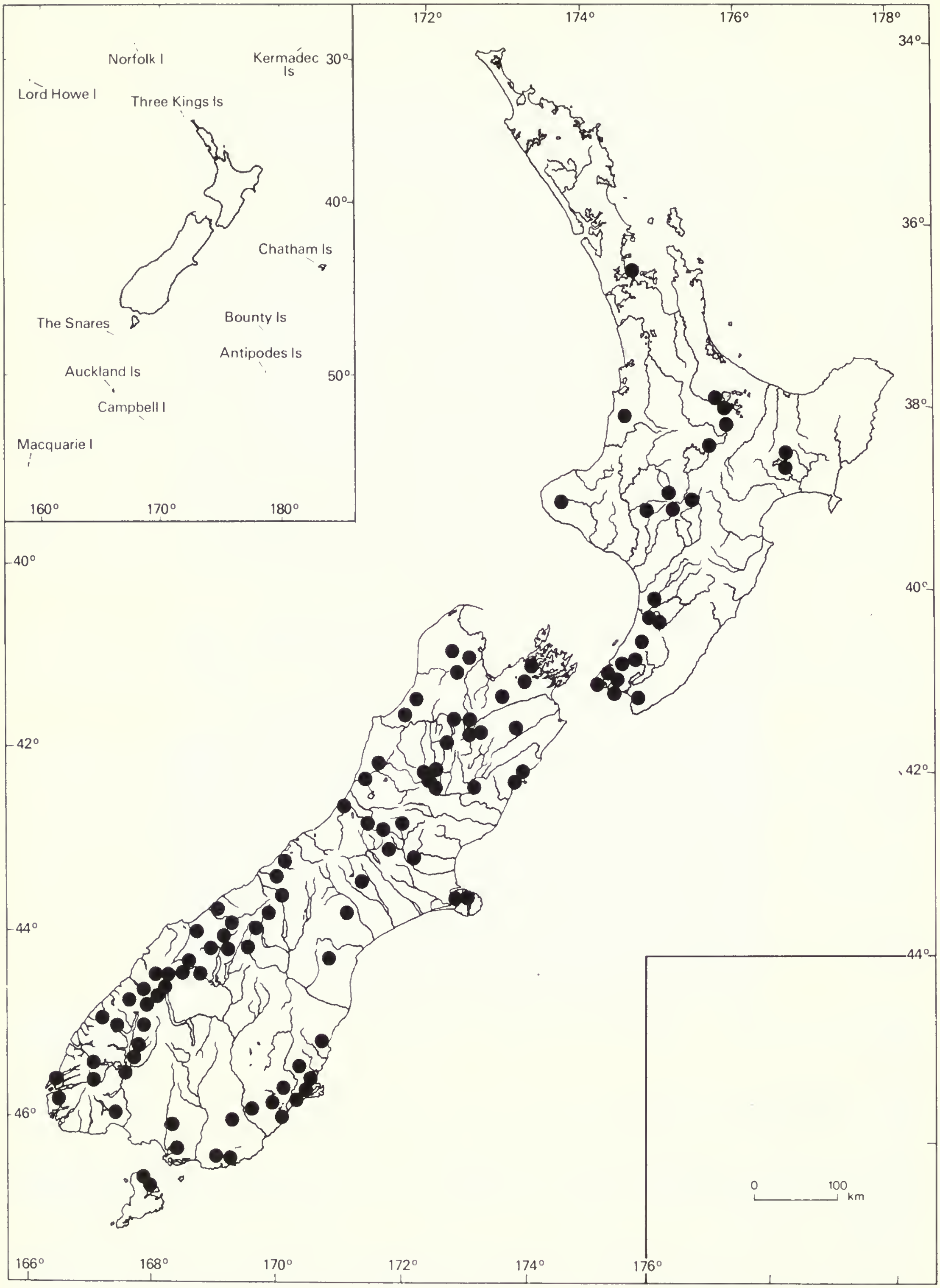
Norfolk I
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Fig. 39 Distribution of *Pseudocyphellaria colensoi*.

light intensities and is thus best developed in open forests, at forest margins, and in the forest canopy. In areas receiving frequent light rain or where mist or cloud cover is common, specimens of *P. colensoi* may reach a great size and contribute a substantial amount to the forest biomass. In humid, partly shaded sites, *P. colensoi* will grow on rocks below shrubs or small trees. It is known from the following phorophytes: *Avicennia marina* var. *resinifera*, *Buddleia* sp., *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Melicytus ramiflorus*, *Metrosideros robusta*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *N. truncata*, *Phyllocladus alpinus*, *Podocarpus hallii*, *P. totara*, *Pseudopanax*, and *Weinmannia racemosa*. Often a dominant epiphyte, it associates with species of *Menegazzia*, *Psoroma*, *Parmelia*, *Pseudocyphellaria*, *Sphaerophorus*, and *Usnea*.

Specimens examined: 400.

11. **Pseudocyphellaria corbettii** D. Galloway, **sp. nov.** **Fig. 40**

Diagnosis: Pseudocyphellariae homoeophyllae similis sed lobis rotundatis, 0·5–2·5 cm latis, margine dense phyllidiatis, phyllidiis teretibus, coralloideus vel squamiformibus, cuneatus, flabellatus vel ± pectinatus. Apothecia ignota. Typus: New Zealand, South Island, Nelson, Red Hills, 1050 m, on *Leptospermum scoparium*, 30 December 1978, *J. K. Bartlett* (BM! – holotype; CHR – isotype). [TLC: 7β-acetoxyhopan-22-ol, hopane-7β-22-diol (tr.), hopane-15α, 22-diol, usnic acid (tr.), hyperstictic (tr.), norstictic, stictic, cryptostictic, constictic acids, and unidentified accessory compounds].

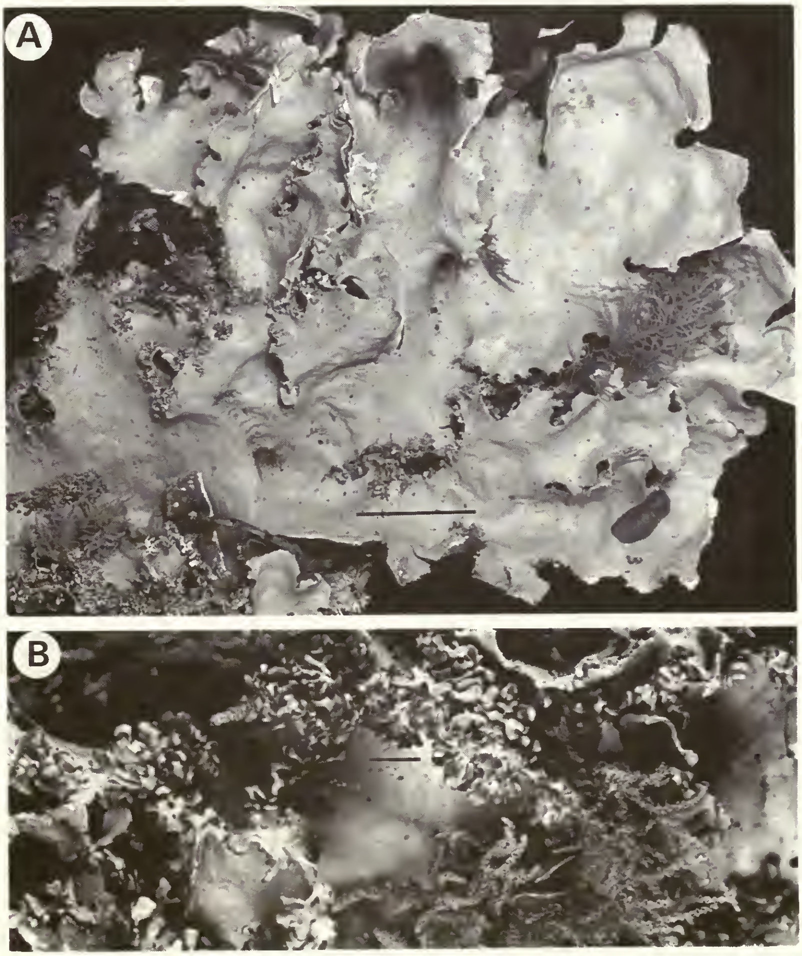

Fig. 40 *Pseudocyphellaria corbettii*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 1 mm.

Morphology: *Thallus* orbicular to irregularly spreading, 5–10 cm diam., corticolous or muscicolous, closely attached centrally, free and ± ascending at apices. *Lobes* broadly rounded, 0·5–2·5 cm diam., discrete at margins, imbricate centrally, plane to irregularly undulate-concave and appearing somewhat cochleate. *Margins* entire in part, to ± irregularly and shallowly crenate or lacerate, becoming phyllidiate, sinuous, ascending in parts, in others ± revolute, slightly thickened, sinuses prominent, semicircular. *Upper surface* lettuce green with a yellowish tinge when moist, pale greenish or greyish yellow or buff, apices suffused red-brown when dry, smooth or minutely wrinkled or impressed, matt, in places with minute solitary or clustered pale fawnish spots or papillae, somewhat coriaceous, without soredia, isidia, maculae or pseudocyphellae. *Phyllidia* mainly marginal, rarely laminal along breaks or tears in thallus or in areas of insect damage, 0·5–1 mm tall, solitary to densely clustered, dorsiventral, rarely ± terete, simple, bifurcating to ± coralloid, cuneate, flabellate to ± pectinate, upper surface concolorous with thallus, apices often inflated, brownish, lower surface pale buff to brown, glabrous or occasionally with small, white, flecklike pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* pale whitish or yellow-buff, glabrous in a ± wide marginal zone, darkening towards centre and there ± densely tomentose, tomentum pale buff to brown, thick, woolly, ragged, entangled, cortex smooth or slightly wrinkled-ridged. *Pseudocyphellae* white, scattered, minute, flecklike close to margins, prominent, excavate 0·5–1·5 mm diam., round to irregular centrally, often with a ± prominent margin, sunk in tomentum, decorticate area plane or ± concave, white, granular. *Apothecia* not seen.

Anatomy: *Thallus* 180–270(–325) μm thick. *Upper cortex* 56–68 μm thick, uppermost 2–3 rows of cells pale straw-yellow, compressed, cells 4–6 μm diam., inner rows of cells larger, walls thinner, 7–15·5 μm diam., more loosely arranged. *Photobiont layer* 34–45 μm thick, *photobiont* green, cells rounded with a prominent gelatinous envelope, to 5 μm diam. *Medulla* 45–150 μm thick, colourless, hyphae 2·5–4 μm diam. *Lower cortex* 34–40 μm thick, outermost cells pale yellow-brown or straw-yellow, 4–7 μm thick, inner cells larger, thin-walled to 14 μm diam. *Tomental hairs* to 5 μm diam. and to 270 μm long, colourless.

Chemistry: as above.

This species is named for Prof R. E. Corbett, Emeritus Professor of Chemistry in the University of Otago, Dudedin, New Zealand, for his researches into the chemistry of New Zealand lichens, and especially of the structural elucidation of hopane, stictane, and lupane triterpenoids in species of *Pseudocyphellaria* from New Zealand.

Distinguishing features: *Pseudocyphellaria corbettii* is a distinctive, endemic phyllidiate species in the *P. freycinetii* group having broadly rounded lobes, a smooth, somewhat coriaceous upper surface with characteristic marginal phyllidia (simple, bifurcate to ± coralloid), a white medulla, green photobiont, and a densely tomentose lower surface with conspicuous, white pseudocyphellae. It has a distinctive chemistry of two hopanes [Code A of Wilkins & James (1979)], the stictic acid assemblage of metabolites, and variable (often trace) amounts of usnic acid in the cortex, the latter imparting a characteristic yellow-green colour to the upper surface. Morphologically and chemically the species is related to *P. glabra*, *P. freycinetii*, and *P. homoeophylla*. It is not known fertile.

Variation: At present the species is known only from two South I., subalpine collections, and so variation in lobe morphology and the development of phyllidia cannot be assessed. *Pseudocyphellaria corbettii* is distinguished from the related South American taxon *P. freycinetti* [larger, more papery lobes, with irregularly indented-lacerate, sinuous margins (see Galloway & James, 1986)], the austral *P. glabra* (marginal and laminal, simple to furcate, terete isidia), and the New Zealand endemic *P. homoeophylla* (longer and narrower lobes with entire, sinuous margins lacking either isidia or phyllidia) by the development of marginal, dorsiventral phyllidia (Fig. 8B).

Distribution: (Fig. 41) At present *P. corbettii* is known only from two localities in Nelson and Canterbury in South I., but is undoubtedly of wider occurrence.

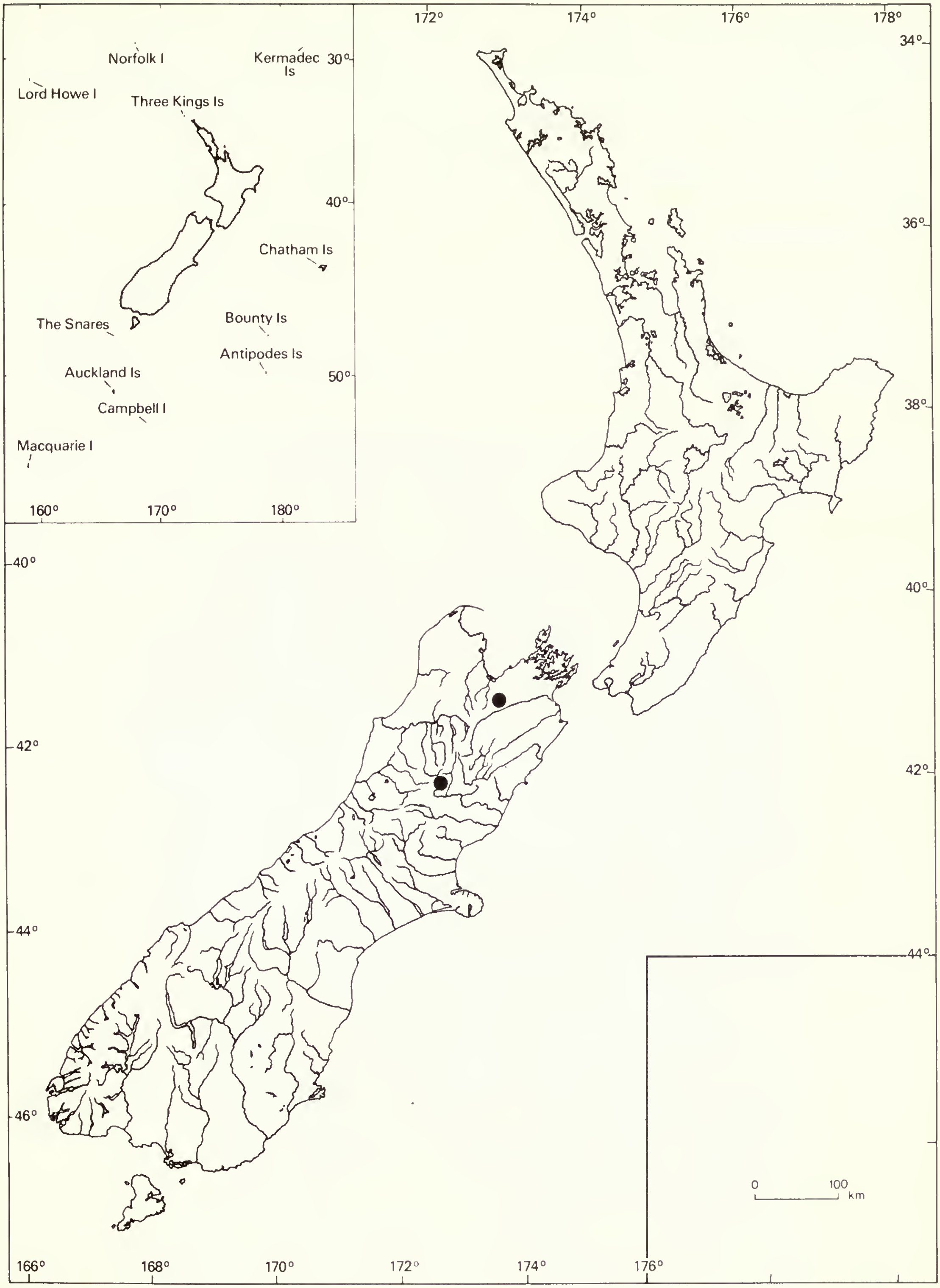
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Fig. 41 Distribution of *Pseudocyphellaria corbettii*.

Habitat ecology: *Pseudocyphellaria corbettii* is a corticolous species known from the bark of *Leptospermum scoparium* (manuka) and *Nothofagus solandri* var. *cliffortioides* (mountain beech) in moderate to high-light habitats at forest margins, where it associates with the lichens *Leptogium azureum*, *Pseudocyphellaria homoeophylla*, *Sticta subcaperata*, *Usnea capillacea*, and *U. xanthophana*. Its detailed ecological requirements are still incompletely known.

Specimens examined: South Island. Nelson: Red Hills, 30 December 1978, *J. K. Bartlett* (BM, CHR). Canterbury: Mt Faust above Boyle River, 11 January 1979, *D. J. Galloway* (BM, CHR).

12. **Pseudocyphellaria coriacea** (J. D. Hook & Taylor) D. Galloway & P. James **Fig. 42**

in *Lichenologist* **12**: 295 (1980). – *Sticta coriacea* J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 648 (1844). – *Ricasolia coriacea* (J. D. Hook. & Taylor) Nyl. in *Mém. Soc. Imp. Sci. nat. Cherbourg* **5**: 103 (1857). – *Lobaria coriacea* (J. D. Hook. & Taylor) Trevisan, *Lichenotheca veneta* exs. 75 (1869). Type: New Zealand, sine loco, *W. Colenso* 3754 (BM! – lectotype).

Sticta subcoriacea Nyl. *Flora, Jena* **48**: 298 (1865). – *Phaeosticta subcoriacea* (Nyl.) Trevisan, *Lichenotheca Veneta* exs. 75 (1869). – *Lobaria subcoriacea* (Nyl.) Hellbom in *Bih. K. svenska Vetensk.* –

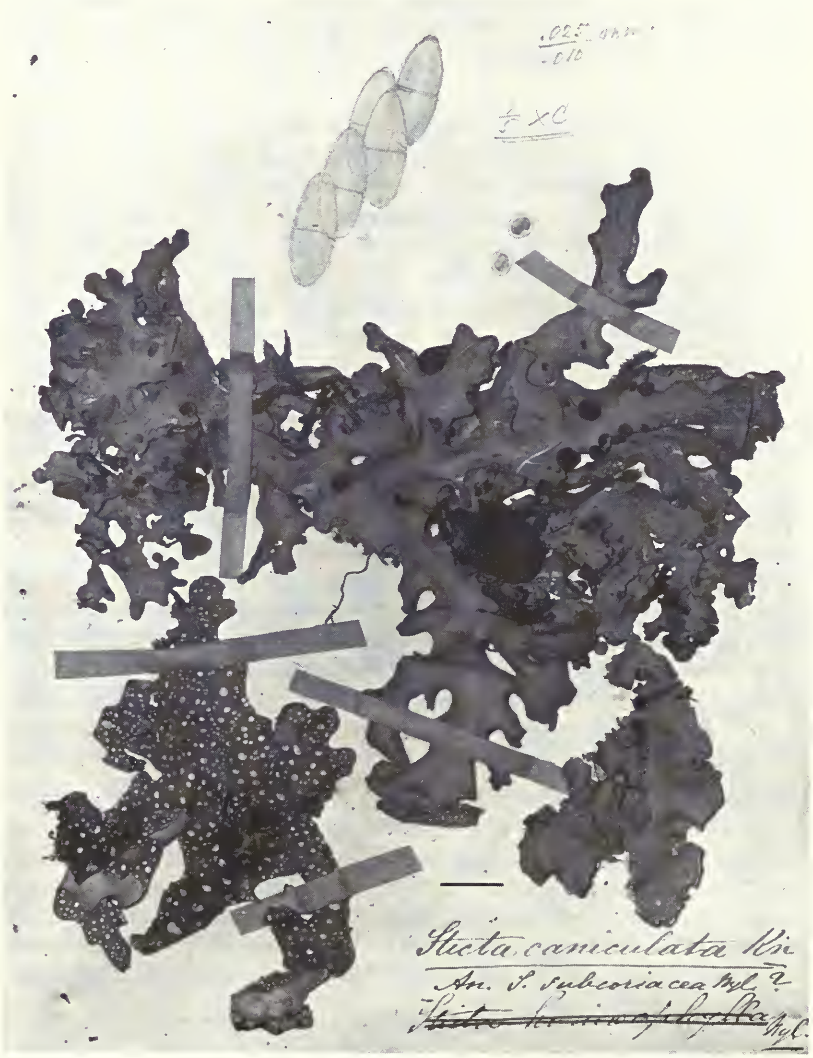

Fig. 42 *Pseudocyphellaria coriacea*. Holotype of *Sticta canaliculata* (WELT). Scale = 1 cm.

Akad. Handl. **21** (3/13): 41 (1896). Type: New Zealand, Otago, Saddle Hill Bush, on trunks of dead trees, 26 October 1861, *W. L. Lindsay* (H-NYL 33660! – holotype: E! – isotype) [see note 1].

Ricasolia coriacea var. *elaphocera* Nyl. in *Bull. Soc. linn. Normandie* **2**: 504 (1868). – *Sticta elaphocera* (Nyl.) Stizenb. in *Flora, Jena* **81**: 113 (1895). – *Lobaria coriacea* var. *elaphocera* (Nyl.) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21** (3/13): 41 (1896). Type: New Zealand, sine loco, *F. V. Hochstetter* 1859 (H-NYL 33376! – holotype) [see note 2].

Sticta canaliculata Knight in *Trans. Linn. Soc. Lond. Bot.* II **1**: 282 (1877). Type: New Zealand, sine loco (? Wellington), *C. Knight* (WELT Herb. Knight Vol. 13A p.11! – holotype; BM!, H-NYL 33659! – ? isotypes) [see note 3].

Sticta coriacea f. *vestitula* Zahlbr. *Denkschr. Akad. Wiss. Wien math.-naturwiss. Kl.* **104**: 282 (1941). Type: New Zealand, North Auckland, Whangarei, on tree trunks, November 1935, *W. A. Given* V 166 (W! – lectotype).

Note 1: *Sticta subcoriacea* Nyl.
This name, given by Nylander to narrow-lobed, elongated specimens of *P. coriacea* first appeared in *Flora* (Nylander, 1865) and not in the paper on Lauder Lindsay's Otago lichens (Nylander, 1866) as recorded in Galloway & James (1980: 295). Nylander's specimen has the following annotation 'On trees: Bush on top of Saddlehill near Dunedin Otago. – New Zealand. Oct. 26, 1861. Dr Lauder Lindsay'.

Note 2: *Ricasolia coriacea* var. *elaphocera* Nyl.
This taxon was described in a footnote (p. 504) to Nylander's *Conspectus synopticus Sticteorum* (Nylander, 1868*b*) where he states that variety *elaphocera* has a thallus branched as in *Sticta damaecornis*, i.e. narrow-lobed and dichotomously branching. Galloway & James (1980: 295) are in error in assigning the name to Nylander (1869).

Note 3: *Sticta canaliculata* Knight
Holotype material of this taxon (Fig. 42) was recently found in Knight's herbarium in New Zealand (WELT), thus making Galloway & James's (1980: 295) typification of the name on BM material incorrect.

Morphology: Thallus orbicular to irregularly spreading, often ± pendulous in well-developed specimens, corticolous, 5–15(–35) cm diam., loosely to closely adnate centrally, free and ± ascending at margins and apices. *Lobes* linear-elongate and rather narrow, straplike, to broad and rounded, ± shallowly concave to markedly canaliculate, 5–15(–20) mm wide, 3–5(–15) cm long, subdichotomously to irregularly branching, discrete or ± contiguous from margins to centre, to complex-imbricate, apices rounded, pointed or ± furcate. *Margins* entire, thickened-ridged below, sinuous, ± ascendent to plane, ± conspicuously white-tomentose. *Upper surface* bright lettuce green, suffused brownish at apices and margins when moist, pale grey-green to buff when dry, becoming brown yellowish- or red-brown on storage, smooth, coriaceous, ± scabrid-areolate in patches, shallowly undulate, occasionally minutely white-pubescent especially towards apices and margins, without soredia, isidia, maculae, phyllidia or pseudocyphellae. *Cephalodia* immersed, visible as small (0·1–1 mm diam.) swellings on upper and lower surfaces. *Medulla* white. *Photobiont* green. *Lower surface* pale buff to chocolate brown, tomentose from margins to centre, tomentum short and ± velvety to long, silky, entangled-arachnoid, white and glistening to grey-buff. *Pseudocyphellae* numerous, starkly white, conspicuous, minute, flecklike, 0·1 mm diam., at margins, centrally 0·4–4 mm diam., ± flat to deeply urceolate, margins distinctly raised, projecting above, or slightly sunk in tomentum. *Pycnidia* sparse to frequent, mainly laminal, scattered, papillate, 0·1–1 mm diam., apical ostiole red-brown to black, punctiform to irregularly fissured. *Apothecia* sessile to subpedicellate, sparse to frequent, mainly marginal or submarginal, occasionally laminal, 0·5–4 mm diam., rounded to irregular, often contorted through mutual pressure, disc pale to dark red-brown, matt, epruinose, exciple pale buff or flesh-coloured, translucent when wet, coarsely corrugate-scabrid, appearing dentate-coronate at margins, thinly pubescent to densely white-tomentose.

Anatomy: Thallus 300–500(–750) µm thick. *Upper cortex* 56–76(–90) µm thick, uppermost 11–14 µm pale red-brown, cells compressed, surface roughened-uneven, remainder colourless or pale straw-yellow, cells 4·5–11·5 µm diam., walls thick. *Photobiont layer* 28–55 µm thick, in irregular, scalloped clumps of densely packed cells, *photobiont* green, cells round, to 7 µm diam. *Medulla* 130–300(–600) µm thick, hyphae 4–5 µm diam., encrusted with colourless, granular crystals. *Lower cortex* 45–50 µm thick, outermost 10–12 µm dilute yellow-brown or straw-yellow, remainder colourless, cells thick-walled, 6–9 μm diam. *Tomental hairs* 45–185 μm long, colourless, single or in fascicles, densely developed. *Apothecia: Exciple* 110–140(–230) μm thick, colourless, cells 4·5–14 μm diam., splitting into pyramidal groups in outer parts (scabrosity). *Hypothecium* pale straw-yellow, 45–65 μm thick, opaque. *Thecium* 90–110 μm tall, colourless; *epithecium* 11·5–18 μm thick, red-brown to yellow-brown overlain by a colourless, amorphous gelatinous layer 9–11·5 μm thick, epithecial pigments turning olive-grey in K, persisting in a band below tips of paraphyses. *Asci* 70–75 × 18–22 μm. *Ascospores* pale yellow-brown to red-brown, broadly ellipsoid, apices pointed, 1-3-septate, locules irregular, middle locule largest, remainder often irregularly lozenge-shaped, 27–30 × 7–9(–11) μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: Pseudocyphellaria coriacea is an endemic species having mainly linear-elongate, rather narrow, straplike lobes which are subdichotomously to irregularly branched, shallowly concave to strongly canaliculate, with enire margins, thickened below and conspicuously white-tomentose. The upper surface is coriaceous, ± scabrid-areolate in parts and occasionally white-tomentose towards apices and margins. It has a white medulla, a green photobiont, and a pale buff to chocolate brown, densely tomentose lower surface with prominent white, abruptly margined pseudocyphellae superficially resembling cyphellae. Apothecia are sessile to subpedicellate, ± marginal, the exciple corrugate-scabrid, thinly pubescent to densely white-tomentose. Epithecium red-brown or yellow-brown turning olive-grey in K. Spores pale yellow-brown to red-brown, 1-3-septate, middle locule largest. The chemistry is two hopanes [Code A of Wilkins & James (1979)].

Variation: There is considerable variation in lobe size in individuals of *P. coriacea* throughout its range in New Zealand, and relatively broad-lobed specimens are collected, as well as long, pendulous, narrow-lobed specimens. Lobes may be plane to markedly canaliculate, but in all cases the ± coriaceous, scabrid-areolate upper surface and the marginal and laminal tomentum are immediately recognizable. *P. coriacea* is one of a small group of endemic species characterized by lobes with white marginal (and/or laminal) pubescence or tomentum. It is distinguished from *P. allanii* which has a blue-green photobiont (see Renner & Galloway, 1982), from *P. fimbriata* which has marginal and occasionally laminal tomentose phyllidia, and from *P. pubescens* which has a ± well-developed laminal tomentum, yellow pseudocyphellae below, white-pruinose apothecial discs, and a differing and distinctive chemistry.

Distribution: (Fig. 43) North Auckland (lat. 34°45′S to Cook Strait in North I., in South I., from Nelson to Southland both east and west of the Main Divide, and in Stewart I., sea-level to 900 m.

Habitat ecology: In the northern part of its range, *P. coriacea* is a common coastal species, being found on tree bark in lowland forest, and on rocks and soil in habitats subject to moderate to high light intensity. Elsewhere, especially in southern beech (*Nothofagus*) forests, it is a prominent epiphyte of forest trees (mainly on trunks, rarely on twigs or in the canopy) and shrubs, most noticeably where light is sufficient, at the forest margin. Also on successional shrubs (especially *Leptospermum*). In Fiordland specimens often reach a great size, probably in response to the favourable growth conditions, especially frequent precipitation, and a high percentage of mist or cloud days throughout the year. Primarily a species of open situations, it will also tolerate moderate shade and in partially shaded habitats it forms photosymbiodemes with *P. allanii.* It is known from the following phorophytes: *Avicennia marina* var. *resinifera*, *Beilschmiedia tawa*, *Cordyline australis*, *Corynocarpus laevigatus*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *M. robusta*, *Myrsine australis*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Pinus radiata*, *Pittosporum eugenioides*, *Podocarpus hallii*, *Prumnopitys ferruginea*, *P. taxifolia*, and *Weinmannia racemosa*.

In northern coastal habitats *P. coriacea* associates with the following lichens: *Heterodermia japonica*, *H. obscurata*, *Psoroma allorhizum*, *P. araneosum*, *Pseudocyphellaria aurata*, *P.*

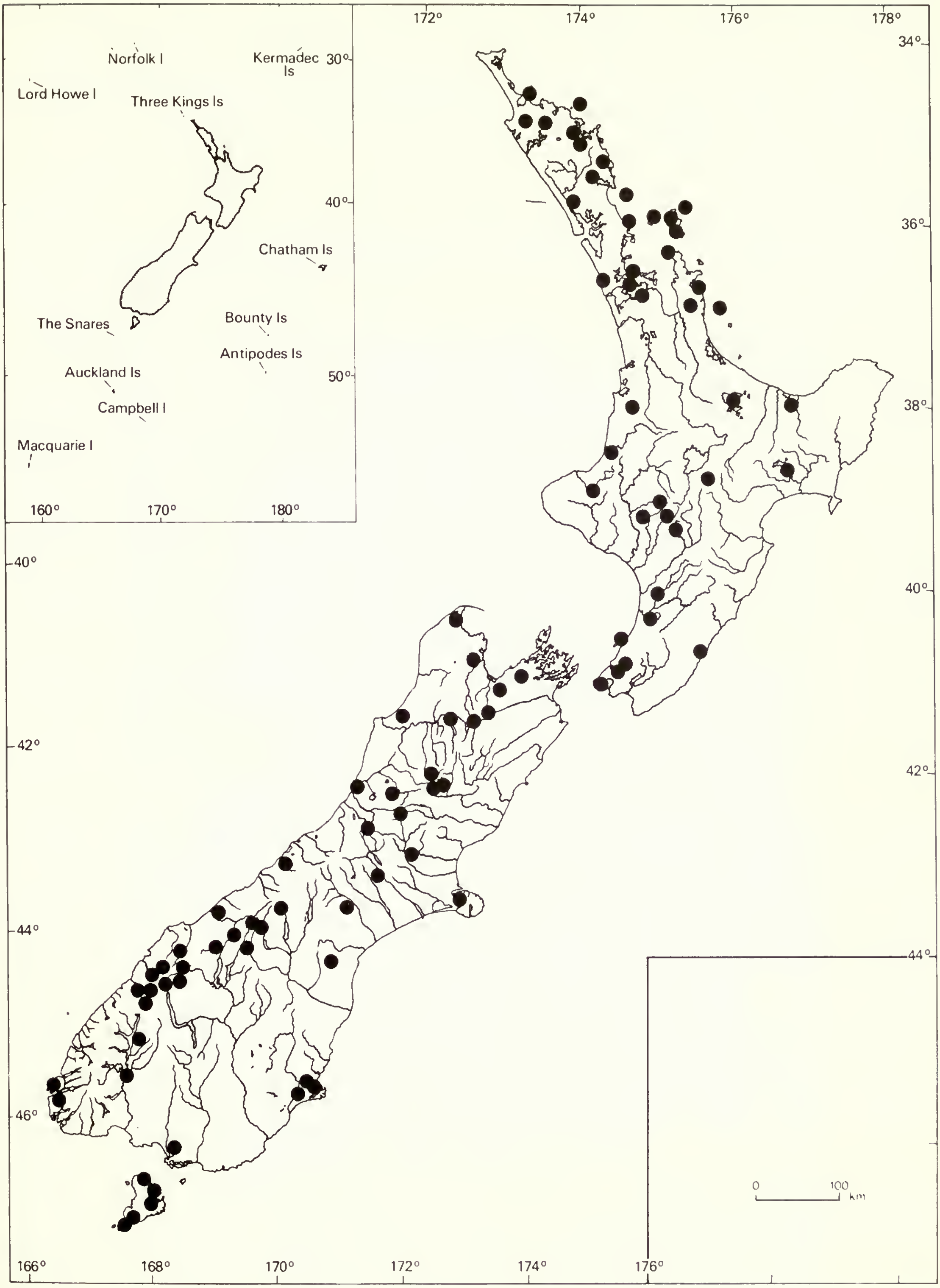
Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
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Fig. 43 Distribution of *Pseudocyphellaria coriacea*.

montagnei, *P. carpoloma*, *Parmotrema chinense*, *P. reticulatum*, and *Usnea rubicunda*.

In southern lowland to subalpine habitats *P. coriacea* associates with: *Anzia jamesii*, *Brigantiaea chrysosticta*, *Lobaria adscripta*, species of *Menegazzia*, *Pseudocyphellaria colensoi*, *P. episticta*, *P. glabra*, *P. homoeophylla*, *P. pickeringii*, *P. pubescens*, and *P. rufovirescens*, species of *Psoroma* and *Sphaerophorus*, *Usnea capillacea*, and *U. xanthophana*.

Specimens examined: 165.

13. **Pseudocyphellaria coronata** (Müll. Arg.) Malme **Fig. 44**

in *Bih. K. svenska Vetensk. - Akad. Handl.* **25** (6): 29 (1899). – *Sticta coronata* Müll. Arg. in *Flora, Jena* **62**: 163 (1879). Type: New Zealand, Greymouth, comm. *F.v. Mueller* (G! – lectotype).

Sticta hirta Stirton in *Rept Trans. Glasgow Soc. Fld. Nat.* **1**: 23 (1873), non *S. hirta* (Nyl.) Trevisan [1869]

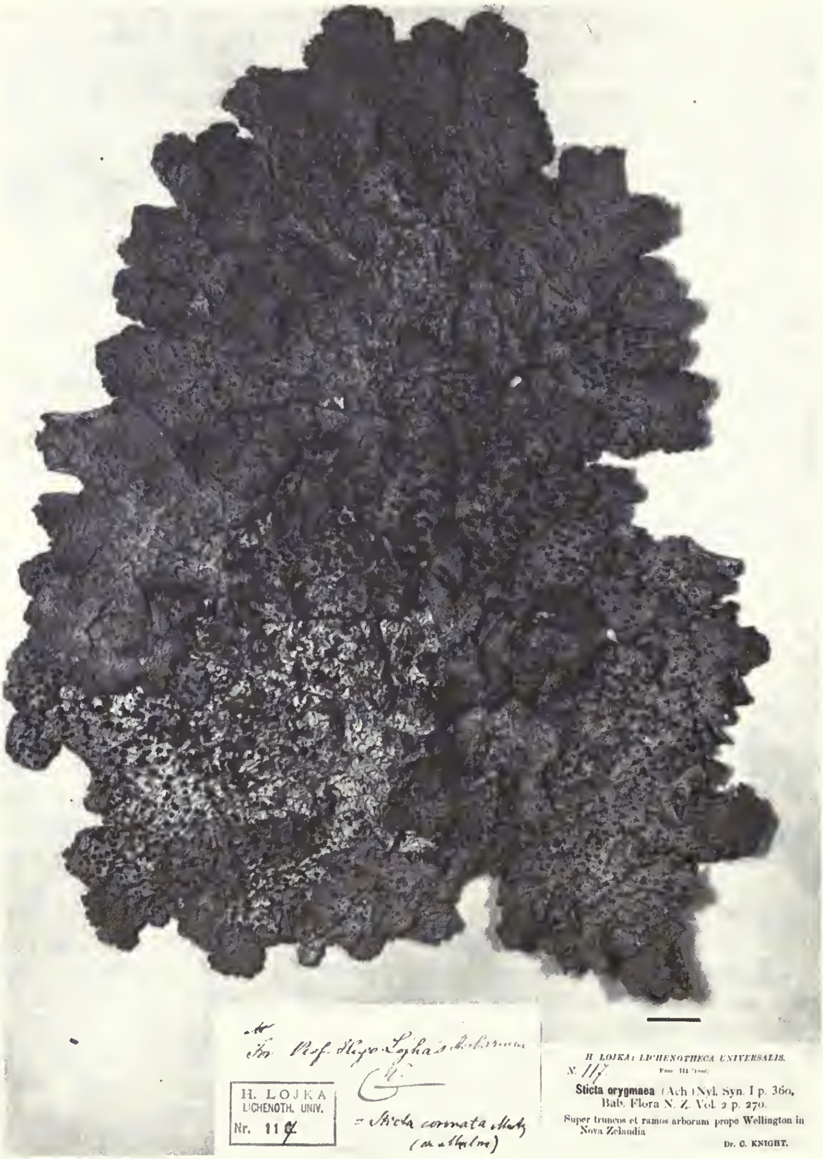
H. LOJKA
LICHENOTH. UNIV.
Nr. 117
= Sticta coronata Müll.
H. LOJKA: LICHENOTHECA UNIVERSALIS.
N. 117
Sticta orygmaea (Ach.) Nyl. Syn. I p. 360, Bab. Flora N. Z. Vol. 2 p. 270.
Super truncos et ramos arborum prope Wellington in Nova Zelandia
Dr. C. KNIGHT.

Fig. 44 *Pseudocyphellaria coronata*. New Zealand, *Knight* (W). Scale = 2 cm.

(Art. 64·1). – *Pseudocyphellaria hirta* D. Galloway & P. James in *Lichenologist* **9**: 95 (1977). Type: New Zealand, Westland, Okarito, January 1872, *J. Buchanan* (OTA! – lectotype).

Sticta orygmaea var. *calvescens* Stirton in *Trans. N.Z. Inst.* **32**: 73 (1900). Type: New Zealand, Wellington, *J. Buchanan* (BM! – lectotype).

In several 19th century accounts this species from New Zealand and the subantarctic islands was known as *Sticta orygmaea* Ach. (see Montagne, 1845; Taylor & Hooker, 1845; Babington, 1855), but this name is a synonym of the South American *Pseudocyphellaria berberina* (Galloway & James, 1977). For a discussion of the synonymy of *P. coronata* see Galloway & James (1977; 1980) and Galloway (1985*b*).

Morphology: Thallus orbicular, rosette-forming, 5–12(–35) cm diam., loosely attached centrally, margins free and often ± subascendent, corticolous, saxicolous. *Lobes* large, rounded, (0·5–)1·5–3(–5) cm wide, ± discrete at apices, complex-imbricate centrally. *Margins* minutely indented, crenate, becoming minutely lobulate to phyllidiate in parts, often densely so in centre of thallus in well-developed specimens. *Upper surface* bright lettuce green, glaucous green with a bluish tinge to yellow-green when moist, pale grey-green or yellow-green when dry becoming cinnamon-brown to tawny and sometimes suffused red-purple on storage, wrinkled-faveolate, faveolae rather small, numerous, shallow or deep, interconnecting ridges short, contorted, sharply defined to smoothly rounded, matt or shining, occasionally minutely scabrid-areolate, often irregularly cracked, without soredia, isidia, maculae or pseudocyphellae, ± consistently phyllidiate. *Phyllidia* occasional to frequent at lobe margins and scattered over, or erupting from lamina of large specimens, also on margins of mature apothecia, delicate, fragile, minute, to 0·2 mm tall, constricted at base, simple to subcoralloid, corticate on upper surface, pale yellow below. *Medulla* yellow, often appearing orange-red in places. *Photobiont* green. *Lower surface* yellow to pale yellow-buff, ± blackened centrally, complexly wrinkled-verrucose to ± bullate, not or sparingly tomentose, tomentum sparse, scattered, in tufts, buff to dark brown, base of apothecia visible as buff brown, glabrous, wrinkled protuberances often sunk below level of lower surface. *Pseudocyphellae* yellow, numerous, 0·1–0·6 mm diam., verruciform-papillate, round to irregular, flat to convex. *Pycnidia* occasional to frequent, scattered or clustered on laminal ridges, minute, 0·1 mm or less diam., papillate to punctiform, black. *Apothecia* sparse to frequent, semi-immersed to sessile, scattered to ± tightly clustered, 0·1–3 mm diam., disc red-brown, matt, epruinose, older fruits occasionally perforate, exciple concolorous with thallus or suffused brownish, margins smooth at first and obscuring disc then becoming coronate-dentate-phyllidiate, phyllidia often eroding and exposing yellow medulla.

Anatomy: Thallus 135–260(–450) μm thick. *Upper cortex* 26–36(–40) μm thick, pale straw-yellow to yellow-brown, uppermost 7 μm of stretched, compressed, necrotic cells, overlying densely compacted thick-walled cells to 4·5 μm diam. *Photobiont layer* 18–22 μm thick, lower margin obscured by granular crystals of medullary hyphae, *photobiont* green, cells rounded, 5–7 μm diam., chloroplast filling most of cell. *Medulla* 65–110(–270) μm thick, hyphae to 4·5 μm diam., densely encrusted with granular red-brown crystals. *Lower cortex* 11–15 μm thick, colourless to pale straw-yellow, cells thick-walled, 3–5 μm diam. *Tomental hairs* colourless, 9 μm thick, 75–200 μm long, rather sparsely scattered. *Apothecia: Exciple* cellular, colourless, 64–90(–185) μm thick, cells 7–9 μm diam., splitting away at margins to form ragged, pyramidal clumps. *Hypothecium* 45–64 μm thick, dilute orange-brown or yellow-brown. *Thecium* colourless to pale straw-yellow, 135–175(–200) μm tall; *epithecium* 10–18 μm thick, minutely granular, red-brown or yellow-brown; *paraphyses* swollen at apices, 4–5 μm thick, apical 3–5 cells ± moniliform. *Asci* 76–90 × 15·5–23 μm. *Ascospores* pale yellow-brown, 1-3-septate, ellipsoid, apices rounded or pointed, straight or curved, cell contents distinctly vacuolate, 32–38·5(–43) × 9 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, polyporic acid, 2α, 3β, 22α-triacetoxystictane, 22α, hydroxystictane-3-one, 2α, 3β-diacetoxystictane-22-ol, stictane-3β, 22α-diol, 2α-acetoxystictane-3β, 22α-diol, 3β-acetoxystictane-2α, 22α-diol, stictane-2α, 3β, 22α-triol, and a range of labile purple or purple-red acidic pigments.

Distinguishing features: Pseudocyphellaria coronata is a large, Australasian species having broadly rounded lobes with minutely indented margins which are often also minutely phyllidiate. The upper surface is ± markedly reticulate-faveolate with mature specimens having scattered, often ± erumpent phyllidia. It has a yellow medulla, a green photobiont, and a pale yellow to ± blackened lower surface which is mainly glabrous and only sparingly tomentose. Apothecia are ± common, small (to 3 mm diam.), semi-immersed to sessile with dentate-phyllidiate margins. Spores are pale yellow-brown, 1-3-septate. The chemistry is characteristic, containing polyporic acid, unidentified pigments (red-magenta in organic solvents), and several stictanes (Murray, 1952; Chin *et al.*, 1973). The pigments in *P. coronata* occasionally impart a purplish colour to thalli in the field, and specimens on long storage in the herbarium may also become ± suffused purple. This phenomenon was observed by Babington (1855: 276) who noted 'Here and there the surface (especially after being wetted) has a delicate purple-violet tint, by which character the species may usually be recognized'; and by Lindsay (1869: 501) who records 'The thallus is frequently stained in patches a beautiful purple, as I have noticed also in various alpine lichens, such as *Platysma cucullatum*, Hoffm., which have a lemon-yellow thallus. I attribute this coloration to the action of the ammonia produced by the decay of the droppings of birds on the colorific principles of the lichen-thallus'.

Variation: *Pseudocyphellaria coronata* is a uniform species and, apart from a wide amplitude of thallus size, the only variables appear to be in the numbers of apothecia and the quantities of phyllidia developed. *Pseudocyphellaria coronata* is most closely related to *P. colensoi*, but is distinguished from it by the rounded, ± regularly reticulate-faveolate lobes, the ± glabrous lower surface, the semi-immersed, small apothecia with coronate-dentate margins, and the red-magenta acetone extract. These characters also differentiate it from *P. degelii*, a non-phyllidiate yellow-medulla species which has a markedly tomentose lower surface, entire lobe margins, sessile to pedicellate apothecia with a well-developed, coarsely-scabrid exciple, and colourless fusiform spores. Its acetone extract is yellow-orange and the medulla contains seco-stictane triterpenoids (Goh *et al.*, 1978).

Distribution: (Fig. 45) North Auckland (lat. 35°20′S) to Cook Strait in North I., and from Nelson to Foveaux Strait in South I. Also on the Chathams, Stewart I., the Snares, the Auckland Is, Antipodes I., and Campbell I., lowland to subalpine, sea-level to 850 m.

Habitat ecology: *Pseudocyphellaria coronata* is an epiphyte of trees and shrubs (it colonizes both twigs and trunks) occurring in a wide variety of habitats from northern coastal forest through lowland beech-podocarp, mixed podocarp-hardwood, to beech (*Nothofagus*) forest to subantarctic lowland forest and subalpine scrub. It is a photophilous species and so reaches its best development in the canopy, on tree trunks in open forest, and at the forest margins in areas of moderate to high rainfall. It is probably the most common and widespread of the corticolous species of *Pseudocyphellaria* in New Zealand, and because of its often great size and beauty (and more recently of its potential as a source of dyestuffs), it has attracted much attention from collectors over the past 150 years. In many forested areas, *P. coronata* is a significant component of the forest ecosytem and contributes substantially to the forest biomass. In humid, semi-shaded habitats *P. coronata* will successfully colonize rocks and stones on the forest floor where there is sufficient light. It is known from the following phorophytes: *Agathis australis*, *Coprosma polymorpha*, *C. pseudocuneata*, *Dacrydium biforme*, *D. cupressinum*, *D. intermedium*, *Dacrycarpus dacrydioides*, *Dracophyllum longifolium*, *D. subulatum*, *D. uniflorum*, *Fuchsia excorticata*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *M. umbellata*, *Myrsine australis*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Phyllocladus alpinus*, *Podocarpus hallii*, *P. totara*, *Rubus australis*, and *Weinmannia racemosa*.

Specimens examined: 325.

14. **Pseudocyphellaria crassa** D. Galloway **Fig. 46**

in *Lichenologist* **15**: 308 (1983). Type: New Zealand, South I., Nelson, West Bay, Lake Rotoiti, on bark of *Kunzea ericoides*, 15 November 1977, *D. J. Galloway* (CHR 381001! – holotype, BM! – isotype).

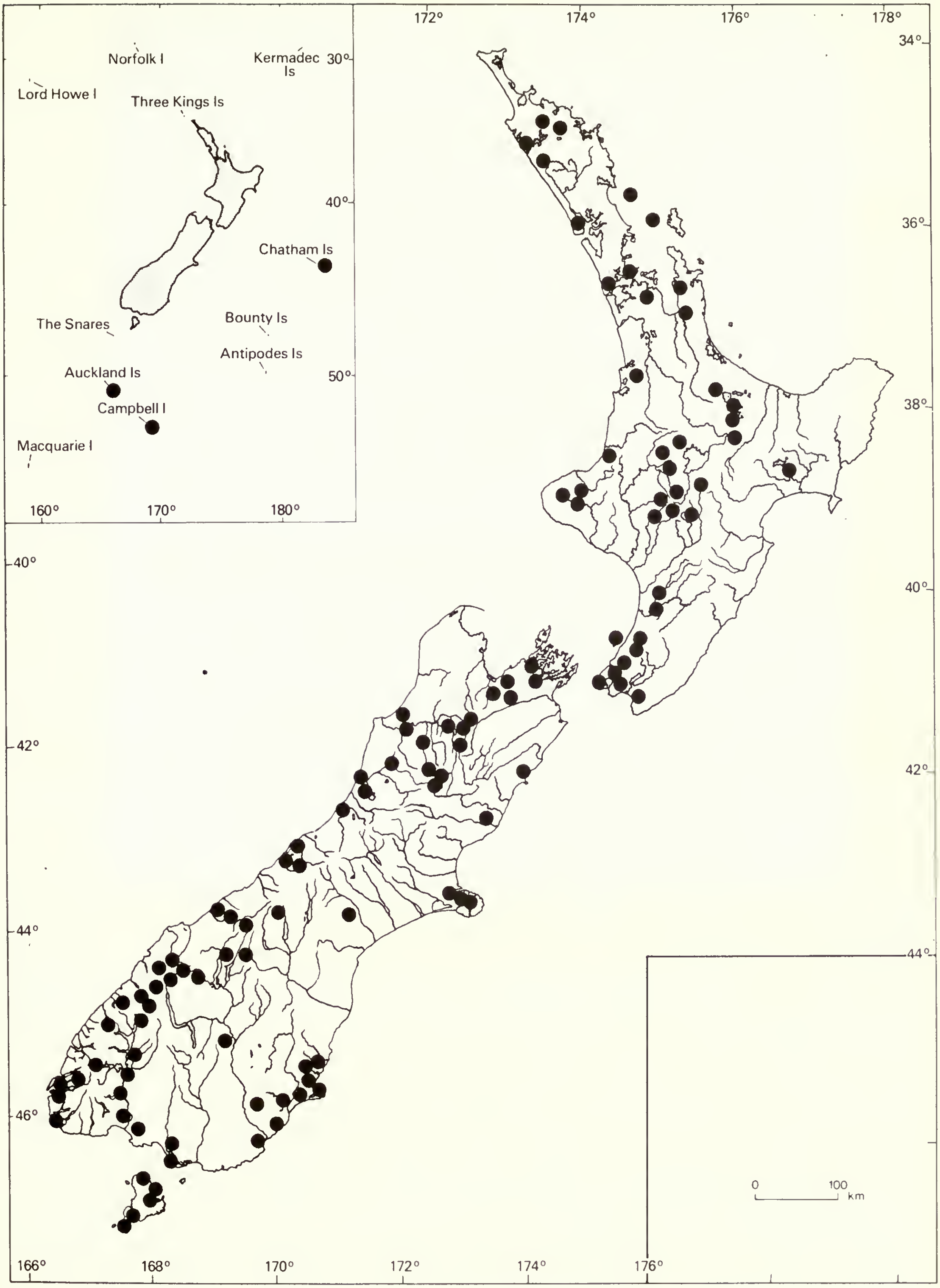
Norfolk I
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Fig. 45 Distribution of *Pseudocyphellaria coronata*.

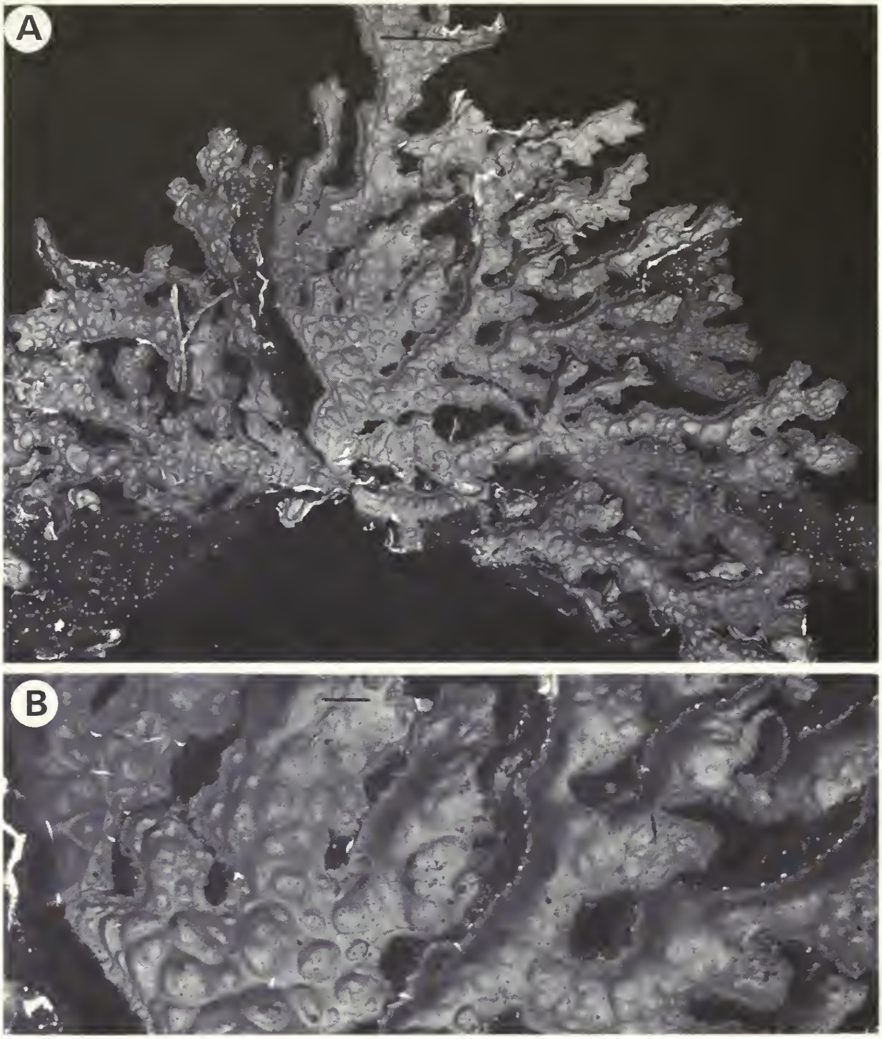


Fig. 46 *Pseudocyphellaria crassa*. Isotype (BM). A. Scale = 1 cm. B. Scale. = 1 mm.

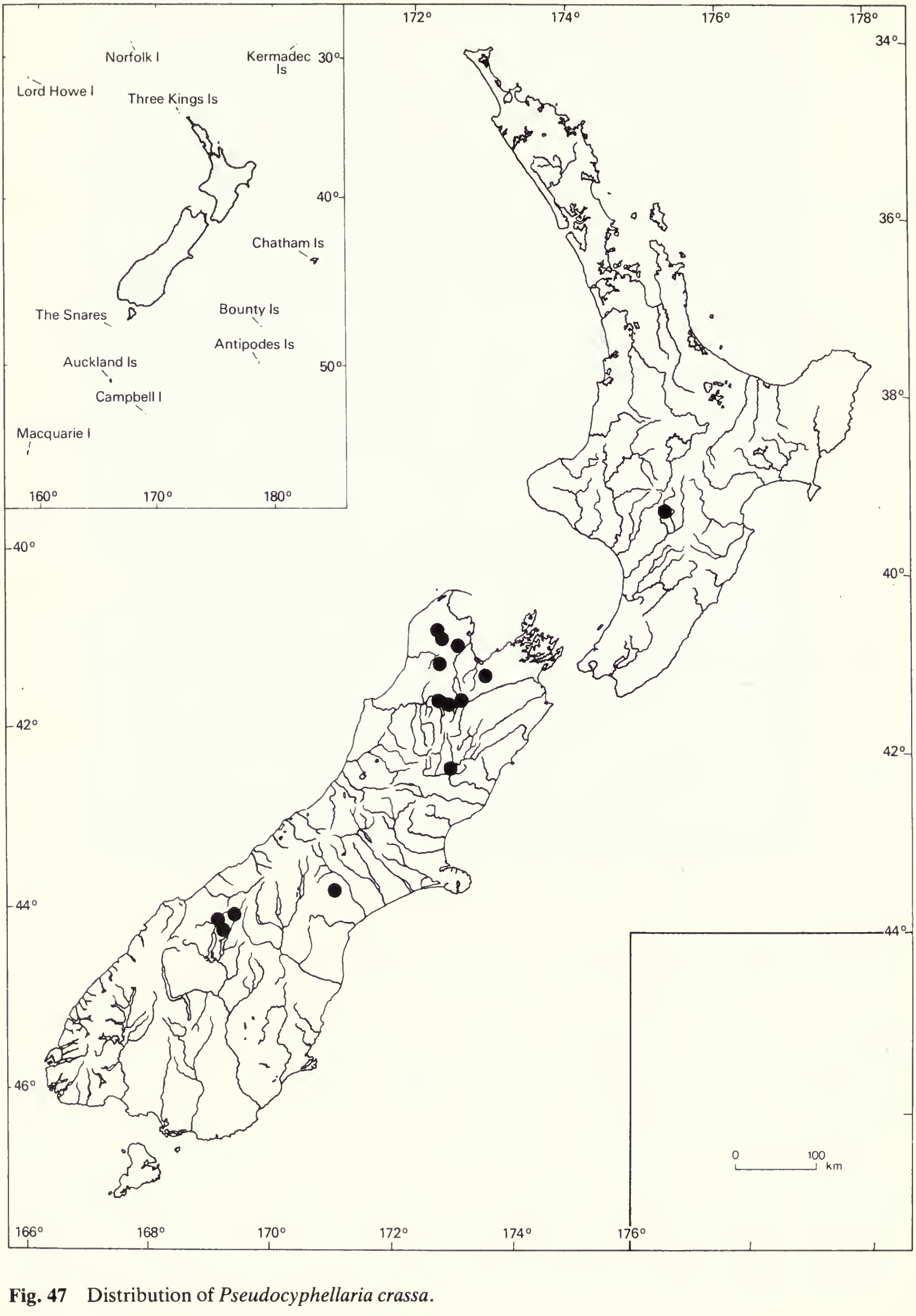
Morphology: *Thallus* orbicular to irregularly spreading, 6–12(–20) cm diam., loosely to tightly adnate centrally, margins free and spreading, ± ascending, corticolous. *Lobes* linear-elongate, 4–8(-15) mm wide, 2–5(–10) cm long, subdichotomously to irregularly branching, apices discrete, contiguous from margins to centre or ± imbricate centrally, convex to plane, apices acute, truncate or ± furcate, sinuses semicircular. *Margins* entire to minutely notched or incised in parts, often minutely papillate and patchily tomentose, ± sinuous, subascendent, markedly thickened above and below, with occasional, punctate, yellow pseudocyphellae, projecting dark tomentum of lower surface often visible as a fringe. *Upper surface* livid greyish blue, suffused reddish or red-brown when moist, pale grey, grey-buff, brownish or red-brown when dry, irregularly reticulate-faveolate, uneven, lacunae deep or shallow, interconnecting ridges sharply defined to smoothly rounded, coriaceous, glossy in parts, matt in others, rarely minutely scabrid-areolate or patchily tomentose towards apices, soredia, isidia, maculae, phyllidia, and pseudocyphellae absent. *Medulla* white. *Photobiont Nostoc. Lower surface* densely and thickly tomentose from margins to centre, tomentum woolly, entangled, red-brown to dark chocolate brown, apices whitish. *Pseudocyphellae* vivid yellow, conspicuous, moderately common to frequent, raised above or slightly sunk in tomentum, papillate-verruciform, round to irregular, 0·1–1 mm diam., decorticate area flat or convex, margins conspicuous, slightly raised, red-brown to ± black. *Pycnidia* sparse to frequent, mainly laminal, hemispherical, 0·2–0·5 mm diam., central ostiole black, minute, punctate-impressed. *Apothecia* sessile, constricted at base, sparse to frequent, marginal or submarginal, concave at first with disc entirely obscured by exciple, plane to convex at maturity, 0·5–3 mm diam., solitary or crowded and slightly contorted through mutual pressure, disc dark red-brown to black, matt, smooth to slightly papillate, epruinose, exciple pale flesh-coloured, ± translucent when moist, coarsely verrucose-scabrid, often slightly tomentose, markedly dentate-coronate at margins of disc.

Anatomy: *Thallus* 180–370(–460) μm thick. *Upper cortex* 45–50 μm thick, upper surface very uneven, with scattered short hairs to 4·5 μm diam. and 11–25 μm tall, upper 11–18 μm dilute orange-brown, remainder colourless, cells thick-walled to 7 μm diam. *Photobiont layer* 45–75 (–82) μm thick, *photobiont Nostoc*, cells 4·5–7 μm diam. *Medulla* 36–73(–230) μm thick, colourless. *Lower cortex* 23–30 μm thick, outermost 7–9 μm dark red-brown, inner zone colourless, cells as in upper cortex. *Tomental hairs* pale straw-yellow to dark brown, to 7 μm thick and 70–350 μm long. *Apothecia:* *Exciple* 80–150 μm thick, colourless, cells thick-walled, 7–18 μm diam., splitting away at margins into irregular, pyramidal clumps (scabrosity). *Hypothecium* 45–55 μm thick, pale yellow-brown, opaque. *Thecium* 100–120 μm tall, colourless to pale straw-yellow; *epithecium* 11–14 μm thick, yellow-brown to olive-brown, unchanged in K, overlain by a thin (4·5–7 μm thick), colourless, amorphous gel; *paraphyses* colourless, capitate at apices which are covered with an olive-brown gel, not dissolving in K. *Asci* 86–108 × 18–20 μm. *Ascospores* olive-brown to dark red-brown, thickened 1-septate to 3-septate, oval-ellipsoid, apices rounded or pointed, septum of 1-septate spores 2–3 μm thick, (23–)25–30 (–32) × 9–11 μm.

Chemistry: Methyl evernate (tr.), tenuiorin, methyl lecanorate (tr.), evernic acid (tr.), gyrophoric acid (tr.), four unidentified depsides (tr.), hopane-7β, 22-diol, hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α-acetoxyhopane-7β, 22-diol (tr.), five unidentified triterpenoids, norstictic (tr.), stictic, cryptostictic, and constictic acids, pulvinic acid, pulvinic dilactone, and calycin.

Distinguishing features: *Pseudocyphellaria crassa* is an endemic species having linear-elongate, subdichotomously to irregularly branching lobes with entire to minutely notched, thickened margins with projecting, punctate, yellow pseudocyphellae; the upper surface is noticeably reticulate-faveolate, the faveolae round to irregular, shallow to deep, without soredia, isidia, maculae, phyllidia or pseudocyphellae. It has a white medulla and a blue-green photobiont. The lower surface is thickly felted-tomentose, red-brown to dark chocolate brown, with conspicuously vivid, yellow pseudocyphellae. Apothecia are marginal, occasional to frequent, the disc dark red-brown to black, epruinose, with a coarsely verrucose-scabrid, dentate-coronate exciple. Spores are olive-brown to dark red-brown, thickened, 1-septate to 3-septate. It has a complex chemistry [Code D of Wilkins & James (1979)].

Variation: This species shows surprisingly little morphological variation throughout its known range in New Zealand, although the production of apothecia seems not especially common, with the majority of specimens examined being sterile. It is one of a group of species having linear-elongate lobes and a reticulate-faveolate upper surface, though its thick, dark, felted tomentum, yellow pseudocyphellae, and blue-green photobiont clearly set it apart from other taxa in the group (*P. billardierei*, *P. carpoloma*, *P. faveolata*, *P. maculata*, *P. physciospora*, and *P. rufovirescens*). It has a chemistry identical to that of *P. carpoloma*, a green photobiont species most common in northern coastal forest which has thinner lobes and a much less thickly developed tomentum. *Pseudocyphellaria crassa* is distinguished from *P. maculata* (primarily a terricolous, subalpine grassland species) by the thickness of the lobes, the absence of maculae on the upper surface, the dense tomentum of the lower surface, and by the chemistry. *P. crassa* is distinguished from *P. physciospora* by the narrower, thicker lobes, prominent, marginal pseudocyphellae, a thicker, darker tomentum on the lower surface, and a different chemistry. In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Three Kings Is
Chatham Is
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Bounty Is
Antipodes Is
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km

Fig. 47 Distribution of *Pseudocyphellaria crassa*.

earlier accounts (Galloway & Simpson, 1978; Galloway & James, 1980; Galloway *et al.*, 1983*b*) *P. crassa* was incorrectly recorded as *P. neglecta* (see also Galloway, 1983*b*).

Distribution: (Fig. 47) Most commonly collected in New Zealand in North Canterbury and Nelson between lats 41°S and 42°S, but recorded once from Wellington (lat. 39°S) and from Peel Forest, South Canterbury, and from localities near Haast Pass in Otago, from 300–1050 m.

Habitat ecology: Pseudocyphellaria crassa is a subalpine species growing as an epiphyte on successional shrubs and trees (especially *Kunzea* and *Leptospermum*) in mountainous areas of Nelson where it is best developed. It colonizes both bark and twigs of *Kunzea ericoides* and at West Bay, Lake Rotoiti, it is commonly found at the base of this tree and also overgrowing rocks and soil in the vicinity. Apart from *Kunzea* and *Leptospermum*, which seems its preferred substrates, *P. crassa* is known from the following phorophytes: *Aristotelia fruticosa*, *Nothofagus fusca*, *N. menziesii*, *Plagianthus regius*, and *Populus* (Hanmer Springs in an exotic plantation).

Specimens examined: 25.

15. **Pseudocyphellaria crocata** (L.) Vainio **Figs 48, 49**

in *Hedwigia* **37**: 34 (1898). – *Lichen crocatus* L., *Mantissa Alter.*: 310 (1771). – *Lobaria crocata* (L.) Räuschel, *Nomenclat. Bot.* 3rd ed.: 330 (1797). – *Sticta crocata* (L.) Ach., *Meth. Lich.*: 277 (1803). – *Stictina crocata* (L.) Nyl., *Syn. meth. lich.* **1**(2): 338 (1860). – *Saccardoa crocata* (L.) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Cyanisticta crocata* (L.) Gyelnik in *Feddes Reprium Spec. nov. veg.* **29**: 7 (1931). Type: India, sine loco, *König* (LINN 1273. 137! – holotype) [see note 1].

Pulmonaria aurigera Bory *in* Floerke in *Magazin Ges. naturf. Fr. Berl.* **2**: 126 (1809). – *Sticta aurigera* (Bory) Delise in *Mém. Soc. linn. Normandie* **2**: 54 (1825). – *S. mougeotiana* var. *aurigera* (Bory) Nyl., *Syn. meth. lich.* **1** (2): 341 (1860). – *Cyanisticta mougeotiana* var. *aurigera* (Bory) Szatala in *Annls hist.-nat. Mus. natn. Hung.* **7**: 41 (1956) nom. inval. (Art. 33.2). – *Cyanisticta aurigera* (Bory) Dodge in *Beih. Nova Hedwigia* **12**: 171 (1964). Type: Les arbres des forêts montagneuses des Îles de France (Mauritius) et de Mascareigne, Herb. Bory de St-Vincent (PC-THURET! – lectotype) [see note 2].

Sticta aurigera var. *nuda* Delise in *Mém. Soc. linn. Normandie* **2**: 55 pl. 3 fig. 9 (1825). – *Cyanisticta aurigera* var. *nuda* (Delise) Dodge in *Beih. Nova Hedwigia* **12**: 172 (1964). Type: Îles de France (Mauritius) et Mascareigne, ?*Bory de St-Vincent*, ex Herb. Bory (PC-THURET! – lectotype).

Sticta mougeotiana Delise in *Mém. Soc. linn. Normandie* **2**: 62 pl. 5 fig. 13 (1825). – *Stictina mougeotiana* (Delise) Nyl., *Syn. meth. lich.* **1**(2): 340 (1860). – *Pseudocyphellaria mougeotiana* (Delise) Vainio in *Hedwigia* **37**: 36 (1898). – *Merosticta mougeotiana* (Delise) Clements, *Gen. Fungi*: 175 (1909). – *Cyanisticta mougeotiana* (Delise) Dodge in *Beih. Nova Hedwigia* **12**: 177 (1964). Type: Île de France (Mauritius), *Bory de St-Vincent* (PC-THURET! – lectotype) [see note 3].

Sticta mougeotiana var. *xantholoma* Delise in *Mém. Soc. linn. Normandie* **2**: 63 pl. 5 fig. 14 (1825). – *Stictina mougeotiana* var. *xantholoma* (Delise) Nyl. *Syn. meth. lich.* **1**(2): 340 (1860). – *Pseudocyphellaria xantholoma* (Delise) Dodge, *Hancock Pacific Expeditions* **3**: 37 (1936). – *Cyanisticta xantholoma* (Delise) Dodge in *Beih. Nova Hedwigia* **12**: 178 (1964). Type: Ex Insulae Borboniae ou Franciae, sine collectoribus nomine (PC-LENORMAND! – lectotype).

Sticta leucosticta Pers. *in* Gaudichaud, *Voy. Uranie Bot.*: 200 (1827). – *Stictina crocata* f. *leucosticta* (Pers.) Nyl. *in* Hue in *Nouv. Archs Mus. Hist. nat. Paris.* **3**,2: 296 (1890). – *Sticta crocata* f. *leucosticta* (Pers.) Zahlbr., *Cat. Lich. Univ.* **3**: 378 (1925). Type: In insulis Sandwicensibus [Hawaii] (ad truncos), *Gaudichaud* (not seen).

Sticta xanthosticta Pers. *in* Gaudichaud, *Voy. Uranie Bot.*: 201 (1827). Type: In insulis Sandwicensibus (ad arborum truncos), *Gaudichaud* (not seen).

Sticta citrina Pers. *in* Gaudichaud, *Voy. Uranie Bot.*: 201 (1827). – *S. crocata* f. *citrina* (Pers.) Zahlbr., *Cat. Lich. Univ.* **3**: 377 (1925). – *Cyanisticta citrina* (Pers.) Gyelnik in *Feddes Reprium Spec. nov. veg.* **29**: 7 (1931). Type: In insulis Maclovinus [Falkland Islands] (obtegit rupes), *Gaudichaud* (not seen).

Cyanisticta subcrocata Gyelnik in *Feddes Reprium Spec. nov. veg.* **29**: 7 (1931). Type: Africa australis (*Drège*, sub *St. crocata* v. *gilva*, pr. p. Spec. orig. in herb. mus. nat. hist. Wien) (not seen).

Cyanisticta epiflavoides Gyelnik in *Annls Cryptog. exot.* **4**: 170 (1931). Type: U.S.A., Maine, Mt Desert Island, Witch Hole, on maple, *C. C. Plitt* 7–20–28. (BP – not seen).

Cyanisticta positiva Gyelnik in *Rév. Bryol. Lichénol.* **5**: 31 (1932). Type: U.S.A., Maine, Mt Desert Island, Witch Hole, on tree trunk, *Plitt*, sub *Sticta crocata* (BP herb. Szatala – not seen).

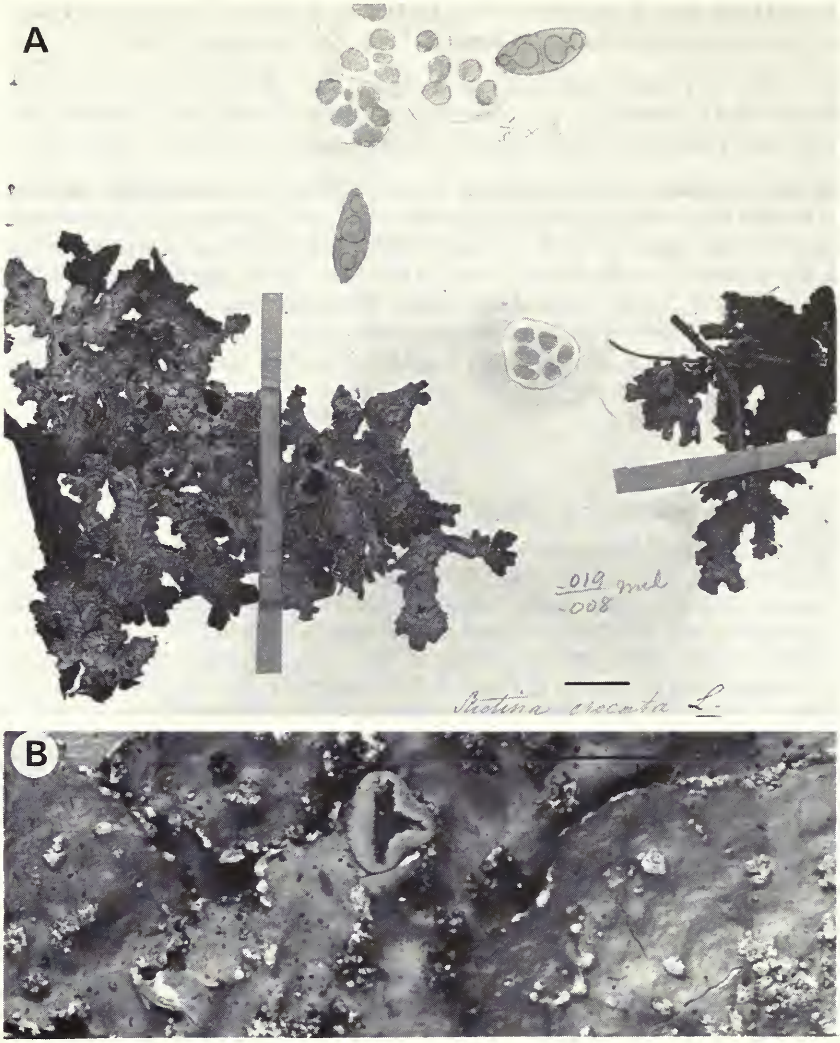


Fig. 48 *Pseudocyphellaria crocata*. A. New Zealand, *Knight* (WELT). Scale = 1 cm. B. Rangitoto Island, *Allan* W1(W). Scale = 2 mm.

Note 1: *Pseudocyphellaria crocata* (L.) Vainio
Pseudocyphellaria crocata is based on Linnaeus's *Lichen crocatus*, a name given to an Indian plant collected by König (see Galloway & James, 1980: 296, fig. 2). The type has a smooth, shining surface with only slight faveolation visible; the lobes are narrow and much divided, rather sinuous with irregularly raised sorediate margins; the soralia are golden yellow, farinose, and are also sparingly present on the upper surface.

Note 2: *Pulmonaria aurigera* Bory
Pulmonaria aurigera is a synonym of *Pseudocyphellaria crocata.* It has a relatively broad-lobed, undulating, but not faveolate-ridged thallus (Fig. 49) with prominent, yellow, notably delimited (i.e. not in any reticulate or confluent pattern), marginal and laminal soralia. In var. *nuda* Delise, the upper surface is slightly ridged-reticulate and the soralia are primarily marginal. The type specimens of both taxa are illustrated and discussed in Galloway & James (1986: figs 11, 12). Delise (1825*a*) is in error in ascribing the basionym of this species to *Lichen aurigerus* Bory (Bory, 1804), and appears not to have seen Floerke's (1809) work where Bory's description of *Pulmonarea aurigera* is validated (see Galloway & James, 1986). Bory's description states 'frondibus laciniato-lobatis submembranaceis, verrucis aureis subtus, supra et in marginibus sparsis'.

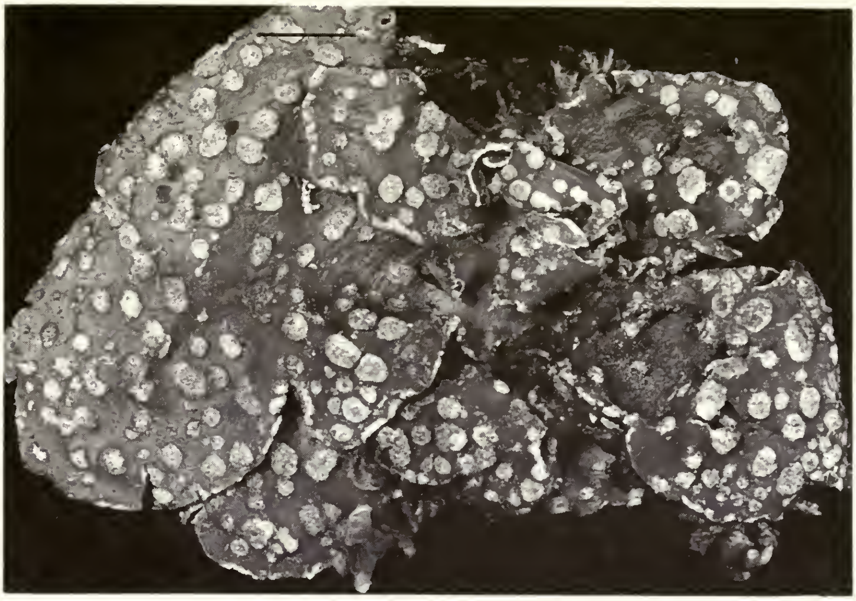


Fig. 49 *Pseudocyphellaria crocata*. North branch of Routeburn, *Galloway* (CHR 367876). Scale = 5 mm.

Note 3: *Sticta mougeotiana* Delise
Sticta mougeotiana closely resembles the holotype of *Lichen crocatus* L., in the Linnean Herbarium (LINN 1273.137). It has an undulate to occasionally ridged, subfaveolate upper surface with mainly marginal yellow soralia, though occasional laminal soralia are found as well. In earlier accounts of New Zealand lichens (e.g. Allan, 1949; Martin & Child, 1972) specimens with long, sinuous, marginally sorediate lobes were referred to this taxon (see also Magnusson, 1940: 19). The types of *Sticta mougeotiana* and the var. *xantholoma* are discussed and illustrated in Galloway & James (1986: figs 26, 27).

Morphology: Thallus very variable in size, shape, and thickness, rosette-forming to irregularly spreading, corticolous, muscicolous, terricolous, and saxicolous, loosely to closely attached centrally, margins ± free. *Lobes* (0·2–)0·5–1(–3·5) cm wide and (1–)3–5(–7) cm long, broad and rounded, ± plane, to narrow, ± canaliculate, deeply laciniate and ± discrete from margins to centre, to imbricate-complex. *Margins* entire, sinuous, ± subascending to indented, ragged, incised, crenulate, slightly thickened below, sorediate, soralia punctiform to linear, often distinctly labriform and eroding lower surface, soredia yellow, farinose to coarsely granular. *Upper surface* pale to dark slate blue, often suffused brownish or reddish when moist, pale fawnish grey to glaucous grey or brownish yellow suffused red or brown in parts or ± completely brownish or red-brown when dry, plane, undulate, shallowly and irregularly wrinkled to densely faveolate, ridges sharply defined to smoothly rounded, smooth, slightly coriaceous, matt to ± shining in parts, occasionally slightly and irregularly short tomentose, without isidia, phyllidia or pseudocyphellae; maculate and sorediate. *Maculae* occasional to frequent, best seen in faveolate specimens, delicate, white, distinctly reticulate, following ridges and in faveolae (use × 10 lens). *Soredia* common, laminal and marginal, very variable, randomly scattered in erose, ± rounded soralia to 3 mm diam., densely farinose yellow, or ± linear-elongate at lobe margins, or erupting from pseudoisidiate warts on laminal ridges, central parts eroding yellow-granular, marginal pseudoisidia granular, brownish, not truly corticate as in *P. desfontainii*, often coalescing in lines along ridges, rarely developing into small, corticate, cochleate lobes. *Medulla* white. *Photobiont Nostoc. Lower surface* pale yellow-white to buff at margins, red-brown to black centrally, wrinkled-undulate to + bullate, tomentose from margins to centre, or with a narrow, glabrous marginal zone, often erose-sorediate, tomentum short, velvety, thin and scattered to thick and woolly, pale buff to dark red-brown or black. *Pseudocyphellae* scattered, occasional to frequent, 0·1–1·2 mm diam., flat to ± convex or very shallowly papillate, sunk in tomentum or slightly projecting above. *Apothecia* occasional to rare or absent, marginal and laminal, solitary or clustered (2–5 together), 0·3–2·5 mm diam., round to irregular through mutual pressure, shallowly to deeply cupuliform, undulate, ± subconcave at maturity, disc pale to dark red-brown, matt, smooth, epruinose, exciple pale flesh pink, translucent when moist, obscuring disc at first, rupturing and leaving an irregular, dentate margin, conspicuously verrucose-areolate, occasionally minutely tomentose towards base.

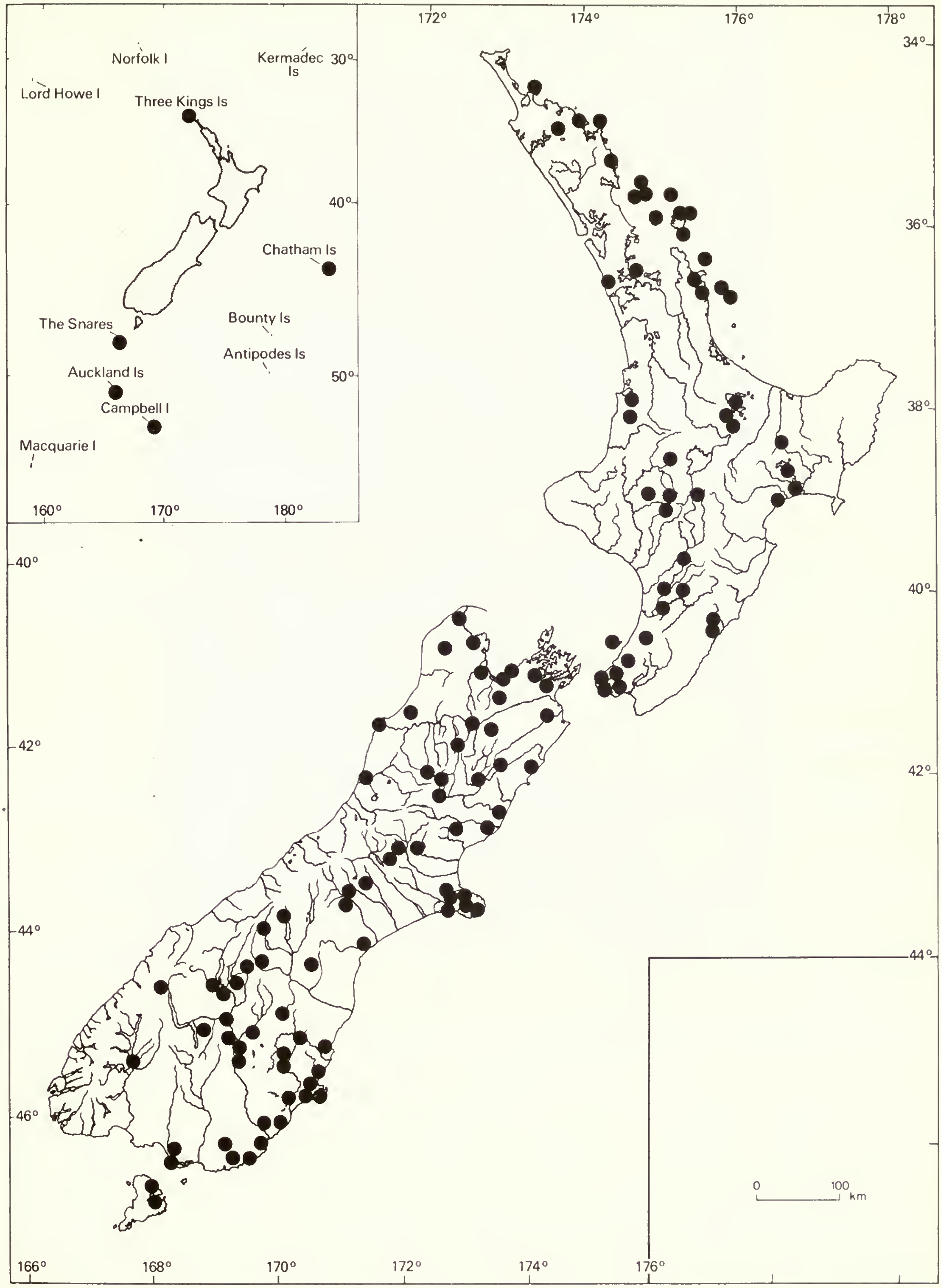
Anatomy: *Thallus* 185–310(–400) μm thick. *Upper cortex* 34–40 μm thick, pale straw-yellow, outermost cells slightly darker, cells thick-walled, 3–7 μm diam. *Photobiont layer* 45–73 μm thick in irregular clumps, *photobiont Nostoc. Medulla* 64–230 μm thick, colourless. *Lower cortex* 23–28 μm thick, pale straw-yellow, outermost layer red-brown, cells 7–11 μm diam. *Tomental hairs* red-brown, 4·5 μm thick, to 140 μm long. *Apothecia: Exciple* colourless, 80–140 μm thick, cells thick-walled, 4·5–15 μm diam. *Hypothecium* 45–65 μm thick, opaque yellow-brown to red-brown, intensifying in K producing sheafs of red crystals (?norstictic acid). *Thecium* colourless to pale straw-yellow, 80–100 μm tall; *epithecium* 11–23 μm thick, dark yellow-brown to olive-brown, pale or dissolving in K. *Asci* 77–82 × 13–15 μm. *Ascospores* broadly ellipsoid, smoky olive-brown to dark brown, thickened 1-septate to irregularly 3-septate, straight or slightly curved, septum of thickened spores variable, 6 μm thick or less, 22·5–27(–29·5) × 9 μm.

Chemistry: A – Tenuiorin, methyl gyrophorate, gyrophoric acid (tr.), hopane-7β, 22-diol (tr.), hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α-acetoxyhopane-7β, 22-diol (tr.), physciosporin (tr.), norstictic (tr.), stictic, cryptostictic (tr.), and constictic acids, pulvinic acid, pulvinic dilactone, and calycin (see Maass, 1975*b*). B – as above but with the replacement of stictic, cryptostictic, and constictic acids by consalazinic and salazinic acids. This latter chemistry occurs in about 20% of specimens examined. These two chemodemes also occur in *P. neglecta*.

Distinguishing features: *Pseudocyphellaria crocata* is a cosmopolitan species having a white medulla, a blue-green photobiont, yellow soralia (both laminal and marginal) on the upper surface, and yellow pseudocyphellae on the lower surface. It has a well-defined chemistry (see above) with two chemodemes present in the total population.

Variation: *Pseudocyphellaria crocata* is probably the most common species of *Pseudocyphellaria* in New Zealand and has a very variable morphology. The two extremes appear to be individuals with broadly rounded lobes (Fig. 49), a ± smooth upper surface, and with marginal and/or scattered, rounded laminal soralia (*aurigera*-type, see Galloway & James, 1986), to individuals with ± linear-elongate, narrow lobes (Fig. 48) and a ± reticulate-faveolate upper surface, with scattered, laminal and/or marginal soralia (*mougeotiana*-type, see Galloway & James, 1986). A complete intergradation exists between these two extremes, and it is often difficult to make a strict segregation of individuals with a ± even, plane surface from those having shallowly to deeply defined faveolae. Soralia are also very variable in both position and density, ranging from exclusively marginal, either labriform, granular-subcorticate or powdery erose-sorediate, to laminal, especially in faveolate forms where soralia are confined to ridges and also to inter-ridge lacunae, to smooth-surfaced forms where soralia are randomly distributed on the upper surface. In contrast to this considerable variation in thallus morphology, the chemistry of the species is remarkably uniform. Colour of the upper surface varies from glaucous-grey in shaded populations to dark red-brown or ± blackened in forms exposed to full sunlight. A large number of the specimens examined (and it is true also for the species in the field) were sterile, though apothecia are occasionally found. As a general rule apothecia in *P. crocata* are produced much less frequently than in the closely related *P. neglecta*.

Pseudocyphellaria crocata is one of a primarily palaeotropical group of species loosely defined by the characters white medulla, blue-green photobiont, and yellow pseudocyphellae (see Magnusson, 1940) but is distinguished from the related endemic species *P. sericeofulva* by lacking the small, imbricate cochleate lobes and the tomentum of the upper surface. Two other taxa may be confused with *P. crocata*: (i) *P. desfontainii* which is similar in all respects to *P.*


Norfolk I
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km

Fig. 50 Distribution of *Pseudocyphellaria crocata*.

crocata but has, instead of soralia, fragile, terete isidia. It is known from South Africa, the islands of the Indian Ocean, Sri Lanka (it is conspecific with *P. ceylonensis* Magnusson), New Caledonia, and north-eastern Australia; (ii) *P. neglecta* (referred to as *P. australiensis* in earlier accounts) which is marginally, occasionally laminally phyllidiate, lacks soralia, and as a general rule tends to form larger, more robust, often copiously fertile, thalli than *P. crocata.* Like this latter species a small proportion of *P. neglecta* have stictic acid replaced by salazinic acid (see Galloway *et al.*, 1983*b*).

Distribution: (Fig. 50) Widespread and common throughout, from the Three Kings Is (lat. 35°6′S) to Campbell I., coastal and inland, sea-level to 1950 m.

Habitat ecology: *Pseudocyphellaria crocata* is a common species of open grasslands and heaths where it is found on rocks or on decorticated wood. It is known from maritime rocks (especially from the offshore islands north of Auckland), from basalt, lava, serpentine, clay banks, and stone walls in drier parts of the country. It is not seen in areas of high rainfall or high cloud cover, preferring drier, open habitats exposed to full sunlight. Although a common coastal species it ascends into high-alpine fellfield on the Remarkables (1950 m), though it is rare or absent from subalpine localities west of the Main Divide. As an epiphyte of trees and shrubs it is most commonly collected from *Cordyline australis* or especially *Leptospermum*. Besides these it is known from the following phorophytes: *Coprosma* spp, *Dacrycarpus dacrydioides*, *Dracophyllum subulatum*, *Metrosideros excelsa*, *Populus*, *Nothofagus solandri* var. *cliffortioides*, *Prumnopitys ferruginea*, *Pseudopanax crassifolius*, *Salix*, and *Weinmannia racemosa*. In Central Otago it is common on schist rocks with *Parmelia signifera*, *P. sulcata*, and species of *Umbilicaria* and *Xanthoparmelia*. Elsewhere in its range it associates with *Everniastrum sorocheilum*, species of *Menegazzia*, *Psoroma*, and *Usnea*, *Sticta fuliginosa* and species of *Pseudocyphellaria*, notably *P. colensoi*, *P. coronata*, *P. dissimilis*, *P. granulata*, *P. neglecta*, *P. pickeringii*, and *P. poculifera*.

Specimens examined: 450.

16. **Pseudocyphellaria degelii** D. Galloway & P. James **Figs 51, 52**

in *Lichenologist* **15**: 141 (1983). Type: New Zealand, South I., Nelson, Mt Haast, on *Nothofagus solandri* var. *cliffortioides* at tree-line, 28 December 1978, *D. J. Galloway* (CHR 381020! – holotype, BM! – isotype).

Morphology: *Thallus* orbicular to irregularly spreading, loosely attached, margins free and ascending to ± unattached, corticolous, musciolous or terricolous, rarely saxicolous. *Lobes* variable, broadly rounded to elongate-laciniate, 0·5–1·5(–3) cm wide and 1–3(–5) cm long, plane to ± canaliculate (especially in grassland forms), discrete to complex-imbricate. *Margins* entire, sinuous, shining, ± thickened or slightly inflated, with scattered, punctate to sublinear, yellow pseudocyphellae, slightly notched in parts, sinuses deeply to shallowly rounded. *Upper surface* bright emerald green, glaucous green or yellow-green occasionally suffused brownish at apices when moist, pale yellow-green or yellow-grey when dry, becoming tawny or ochre-brown on storage, undulate, weakly to strongly wrinkled, pitted, scroliculate or faveolate, interconnecting ridges low, rounded, texture rather thin and papery (grassland forms) to thick, ± coriaceous (bark forms), matt, occasionally minutely scabrid-areolate (use × 10 lens) at lobe apices, occasionally minutely maculate (× 10 lens), without soredia, isidia, phyllidia or pseudocyphellae. *Medulla* yellow. *Photobiont* green. *Lower surface* irregularly wrinkled or puckered, undulate to shallowly bullate, pale yellow to ochre brownish at margins, dark red-brown to blackened centrally, tomentose to margins or with a narrow to broad, glabrous, marginal zone, tomentum often sparse and patchy, ragged to ± dense and woolly, pale whitish grey to brownish, silky. *Pseudocyphellae* yellow, scattered, minute, often somewhat inapparent, 0·05–0·15 mm diam., punctiform to minutely papillate, decorticate area flat to subconvex. *Apothecia* sessile, constricted at base, becoming pedicellate at maturity, pedicel smooth, concolorous with thallus, sparse, often absent from well-developed thalli, (0·5–)1–5(–7) mm

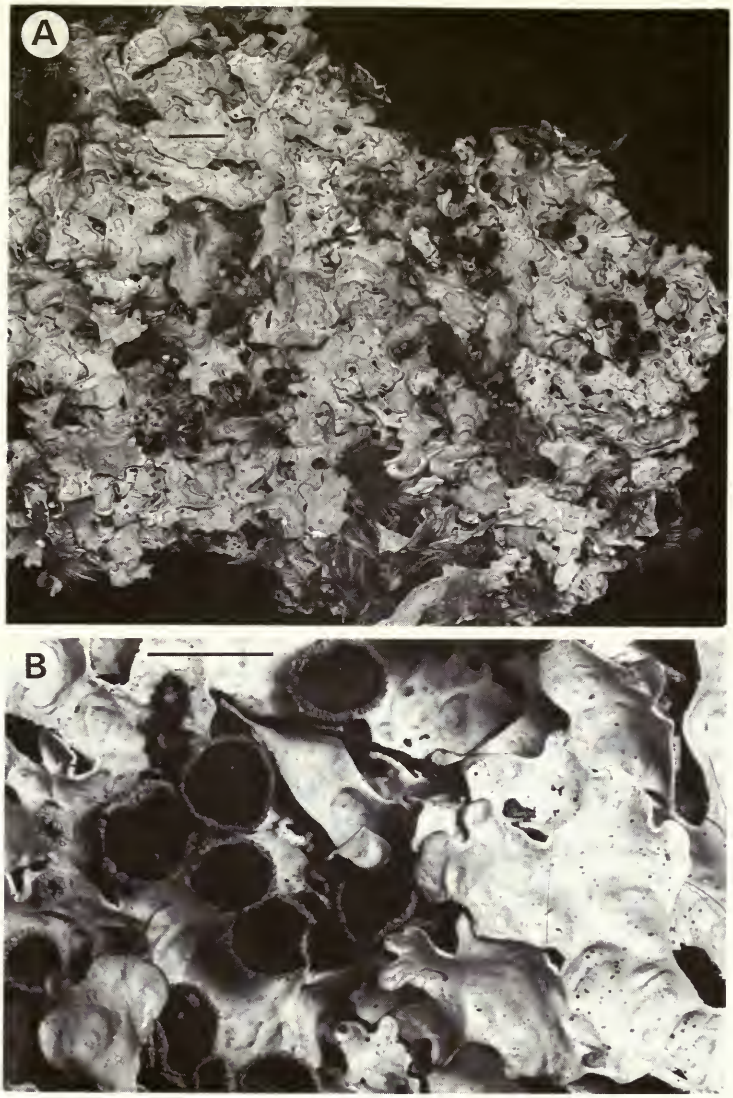

Fig. 51 *Pseudocyphellaria degelii*. Holotype (CHR) A. Scale = 1 cm. B. Scale = 5 mm.

diam., rounded to irregular, concave to plane or ± undulate or irregularly flaring, disc pale to dark red-brown, shining or matt, epruinose, exciple coarsely corrugate-scabrid, areolae deeply delimited, pyramidal, whitish buff to red-brown, translucent when wet.

Anatomy: Thallus 130–200(–250) μm thick. *Upper cortex* 22–27 μm think, upper half dilute yellow-brown to orange-brown, remainder colourless, uppermost layers flattened-compressed, appearing periclinal, innermost cells thick-walled, 4–6 μm diam. *Photobiont layer* 18–30 μm thick, cells densely packed, *photobiont* green, cells to 5 μm diam. *Medulla* 90–140(–170) μm thick, hyphae to 4·5 μm diam., encrusted with yellow crystals especially near photobiont zone and near lower cortex. *Lower cortex* 11–18(–22) μm thick, pale straw-yellow, cells 5–9 μm diam. *Tomental hairs* septate, constricted at septa, pale straw-yellow, to 7 μm diam., 30–120 μm long. *Apothecia*: *Exciple* 130–200 μm thick, cells 6·8–15·5 μm diam., separating in rows near margins as short tomental hairs, or into irregular pyramidal clumps (scabrosity). *Hypothecium* 64–83 μm thick, pale orange-brown, opaque, unchanged in K. *Thecium* 100–110 μm tall, colourless;

epithecium 7–11·5 μm thick, yellow-brown to pale red-brown, granular, colour dissolving in K. *Asci* 85–110 × 15–18 μm. *Ascospores* colourless, fusiform, 1-3-septate, apices pointed, straight or curved, contents of cells often granular-vacuolate, (27–)29·5–36(–40) × (4·5–7–9 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, 22α-hydroxy-3, 4,-secostict-4(23)-ene-3-oic acid, 22α-hydroxy-3, 4-secostict-4(23)-en-3-ol, and 3-acetoxy-3, 4-secostict-4(23)-en-22α-ol (Goh *et al.*, 1978).

Distinguishing features: *Pseudocyphellaria degelii* is a large, endemic species having broadly rounded to linear-elongate lobes with mainly entire margins, lacking isidia, soredia or phyllidia. The upper surface is undulate to scrobiculate or ± strongly reticulate-faveolate, occasionally maculate and scabrid-areolate (× 10 lens). It has a yellow medulla, a green photobiont, and a pale yellow to red-brown or black lower surface with a continuous to patchy tomentum. Apothecia sparse, often absent, sessile to pedicellate, exciple well-developed, coarsely corrugate-scabrid. Spores colourless, fusiform, 1-3-septate. The medulla contains pigments and seco-stictane triterpenoids (Goh *et al.*, 1978).

Variation: *Pseudocyphellaria degelii* has two main growth forms. A corticolous form from near tree-line or at forest margins, has thicker, narrower lobes which are normally wrinkled-scrobiculate to faveolate and which are sparsely fertile (Fig. 51). Subalpine grassland forms, on the other hand, have thinner, broader, and more papery lobes (Fig. 52) which are undulate, smooth, and never or rarely scrobiculate or faveolate, and very rarely fertile. This latter form was recorded in earlier accounts as *Sticta durvillei* (Zahlbruckner, 1941; Allan, 1949), as *Sticta*

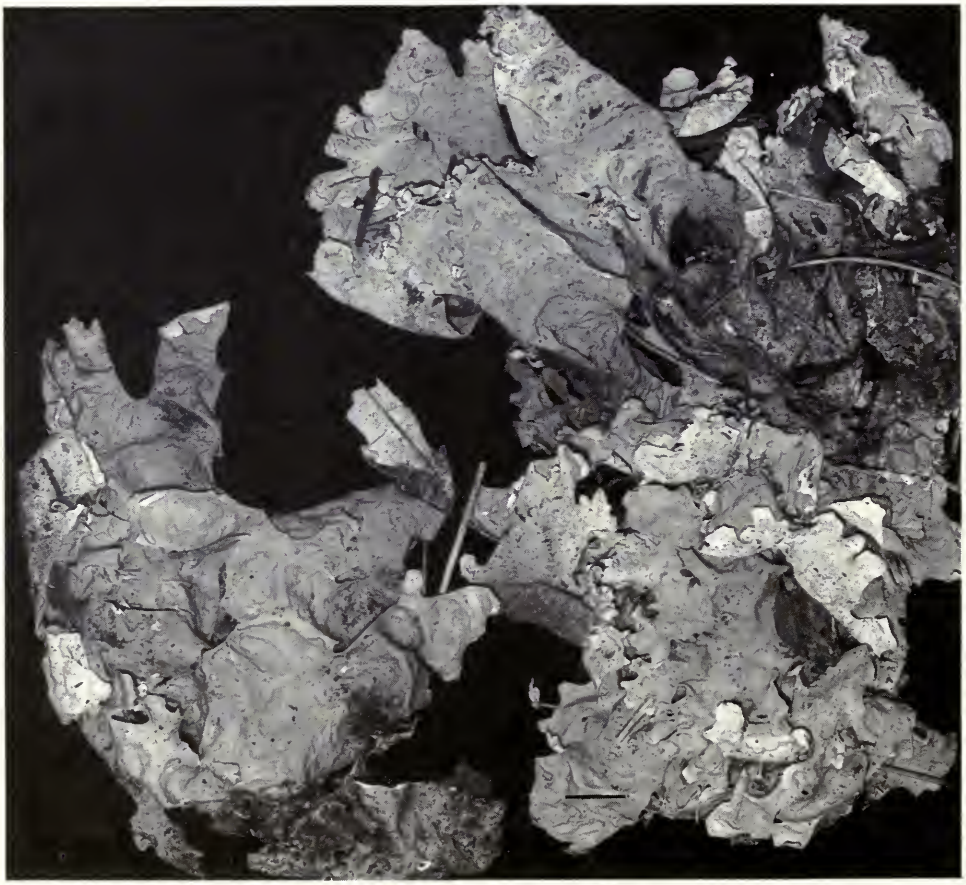

Fig. 52 *Pseudocyphellaria degelii*. Mt Arthur, Nelson, *Bartlett* (CHR 375875). Scale = 1 cm.

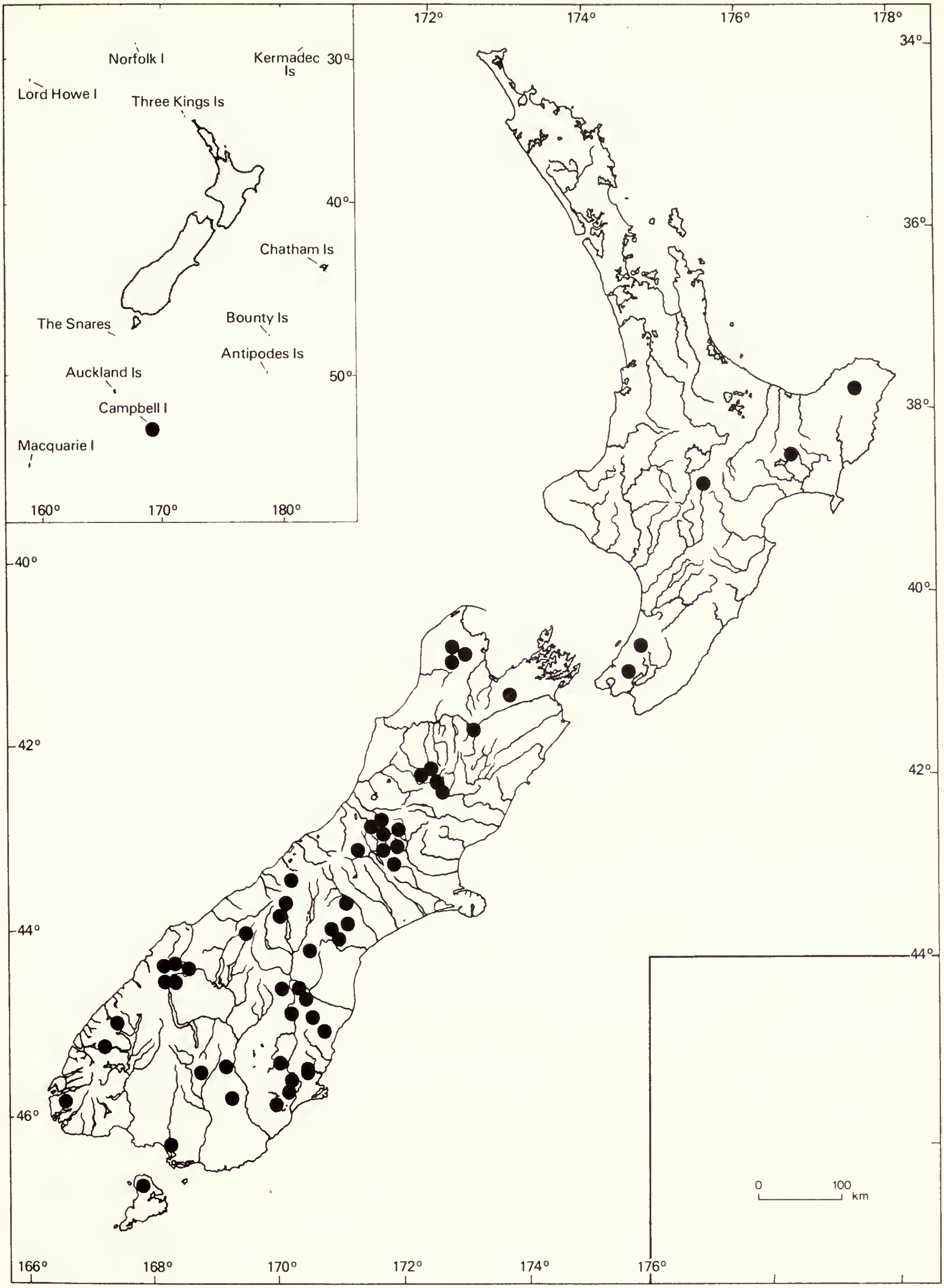
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Fig. 53 Distribution of *Pseudocyphellaria degelii*.

endochrysa (Martin, 1966, 1969*a*; Martin & Child, 1972), and as *P. berberina* (Galloway & James, 1980).

Pseudocyphellaria degelii is readily distinguished from both *P. colensoi* and *P. coronata* on morphological and chemical grounds; it lacks the lacerate margins and marginal and laminal verrucose isidia of *P. colensoi* which has also a yellow acetone extract, and it does not have the broadly rounded lobes of *P. coronata* which are ± glabrous below, or the semi-immersed to sessile and coronate-dentate margined apothecia, or the distinctive red-magenta acetone extract of this species. It appears to be the South Pacific vicariant of the South American taxon *P. berberina* (Galloway & James, 1977), but differs from it in several respects. It is distinctive chemically (Wilkins, 1977*b*; Goh *et al.*, 1978), has narrower lobes which are not as broadly rounded, margins are entire or notched but not conspicuously indented, folded, incised or ± phyllidiate as in *P. berberina*. In *P. degelii* the upper surface is smoother, less deeply faveolate and more rarely scabrid-areolate, and the exciple is also much more massively developed even at an early stage, and is more coarsely areolate-scabrid. Spores in *P. degelii*, (27–)29·5–36(–40) × (4·5–)7–9 μm, are shorter and broader than those of *P. berberina*, (20–)30–50(–55) × (5–)6–7(–8) μm.

Pseudocyphellaria degelii is also distinct from the South American subalpine, subantarctic species *P. endochrysa* and *P. vaccina* (see Galloway, 1986*a*). *P. endochrysa* has a finely pubescent upper surface, broad, papery lobes with linear, marginal pseudocyphellae below, and *P. vaccina* has a distinctive scabrid-areolate upper surface with thickened, inflexed margins without linear marginal pseudocyphellae below. Both these latter species have colourless, acicular spores *c.* 20–32 × 2·5–4 μm.

Distribution: (Fig. 53) From lat. 37°40′S in North I., (Raukumara Range, Huiarau Range, Kaimanawa Range, Tararua Range), and from Nelson to Fiordland in South I., close to the Main Divide and eastwards on foothill ranges of Marlborough, Canterbury, and Otago to Silver Peaks and Mt Maungatua near Dunedin, the Blue Mountains, Forest Hill, and Waihopai Scenic Reserve (Invercargill). Also on Stewart I. (Mt Anglem) and Campbell I. (Mt Azimuth, 395 m), rarely at sea-level, most often from 450–1800 m.

Habitat ecology: Pseudocyphellaria degelii occurs in canopy branches and on trunks of *Nothofagus solandri* var. *cliffortioides* and *Podocarpus hallii*, and is most noticeable at, or near, treeline. In subalpine grassland dominated by species of *Chionochloa*, *P. degelii* is found at the bases of low shrubs (species of *Cassinia*, *Coprosma*, *Dracophyllum*, and *Hebe*) and around tussock bases, and among alpine herbs, predominantly species of *Aciphylla* and *Celmisia*. It is also known from damp soil among rocks or boulders in fellfield. In subalpine grassland habitats and in the higher, more restricted alpine tundra environments (see Mark & Bliss 1970; Bliss & Mark, 1974), *P. degelii* associates with the following lichens: *Alectoria nigricans*, *Cetraria delisei*, *C. islandica* ssp. *antarctica*, *Coelocaulon aculeatum*, *Haematomma babingtonii*, *Hypogymnia lugubris*, *Lecanora broccha*, *L. flavopallida*, *Menegazzia aeneofusca*, *M. castanea*, *M. inflata*, *M. nothofagi*, *M. testacea*, *Pseudocyphellaria maculata*, *Psoroma hirsutulum*, *Siphula decumbens*, *S. foliacea*, *S. fragilis*, *Sphaerophorus tener*, *Sticta martinii*, *Thamnolia vermicularis*, and *Usnea contexta*.

Corticolous associates of *P. degelii* include: *Degelia duplomarginata*, *Parmelia testacea*, *Lecanora atra*, *Haematomma hilare*, *Pseudocyphellaria ardesiaca*, *P. faveolata*, *P. glabra*, *P. homoeophylla*, *Menegazzia pertransita*, *M. dielsii*, *Usnea capillacea*, and *U. xanthophana*.

Specimens examined: 80.

17. **Pseudocyphellaria dissimilis** (Nyl.) D. Galloway & P. James **Fig. 54**

in *Lichenologist* **12**: 297 (1980). – *Stictina fragillima* var. *dissimilis* Nyl., *Syn. meth. lich.* **1** (2): 336 (1860). – *Stictina dissimilis* (Nyl.) Nyl. *in* Lindsay in *Trans. Linn. Soc. Lond.* **25**: 506 (1866). – *Sticta fragillima* var. *dissimilis* (Nyl.) Krempelh., *Reise Oest. Freg. Novara Bot.* **1**: 119 (1870). – *Cyanisticta dissimilis* (Nyl.) Räsänen in *J. Jap. Bot.* **16**: 143 (1940). Type: Australia, sine loco, *Hampe* (H-NYL 34103! – lectotype) [see note 1].

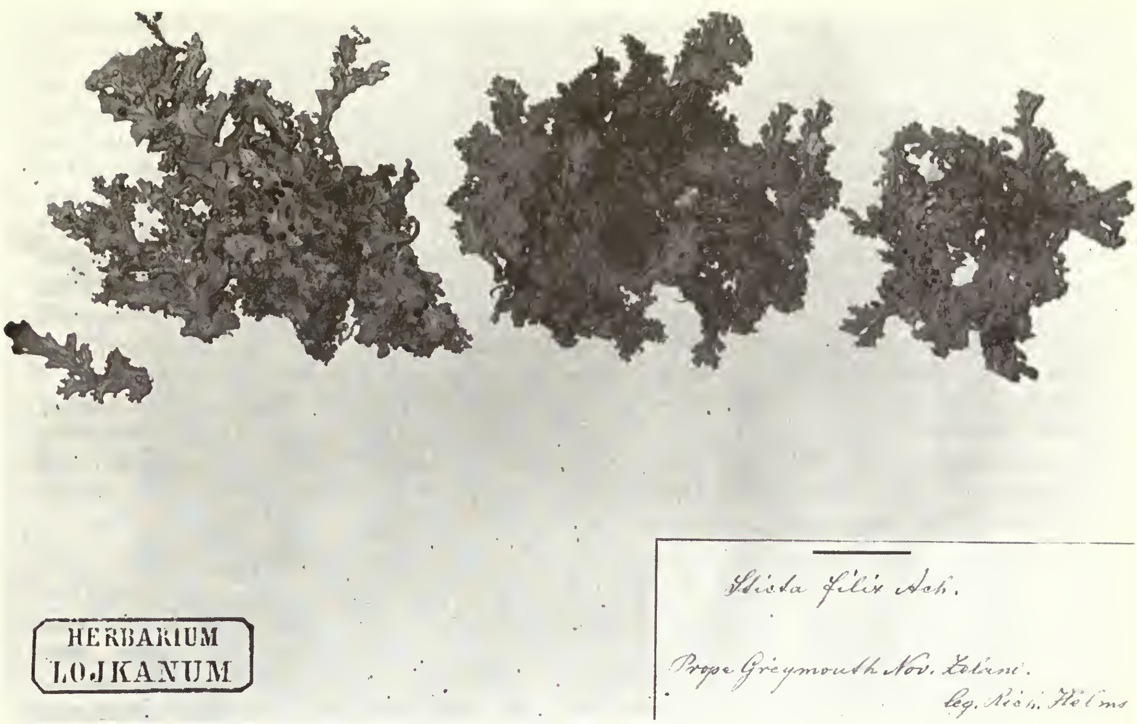

Fig. 54 *Pseudocyphellaria dissimilis*. New Zealand, *Helms* [as *Sticta filix*] (W). Scale = 2 cm.

Stictina fragillima var. *dissecta* Müll. Arg. in *Flora, Jena* **66**: 22 (1883). – *Sticta fragillima* var. *dissecta* (Müll. Arg.) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21**(3/13): 32 (1896). Type: Norfolk Island, *Dr Woolls* (G! – lectotype).

Sticta intricata var. *fimbriata* Zahlbr. in *Denkschr. Akad. Wiss. Wien math.-naturwiss. Kl.* **104**: 290 (1941). Type: New Zealand, Wellington, Totara Reserve, Pohangina River, on *Podocarpus totara*, 31 January 1935, *H. H. Allan* v 186 (W! – lectotype).

Note 1: *Stictina fragillima* var. *dissimilis* Nyl.
In proposing a variety (*dissimilis*) of *Stictina fragillima*, Nylander (1860*b* 336) wrote '-Varietatem hujus (ni fallor), in hb. Hampeano vidi, laciniis thallinis supra medio canaliculato-impressis et margine hinc inde minute laciniato-dissectis; ex Australia Felici et Tasmania. Dicatur var. *dissimilis*. Plerumque lacinias thallinas typo breviores latiores et magis irregulares habet; margines saepe adscendentes'.

The lectotype, H-NYL 34103, chosen by Galloway & James (1980: 297) is only a fragment, as are many of Nylander's specimens retained from larger collections sent to him for determination. The remainder of the Hampe collection has not been located. The type, which is sufficient for identification, is a single sterile lobe (3·5 × 0·5 cm) with small, terete isidia developed at the margins. It is attached to a sheet annotated by Nylander' Sticta fragillima var. Austr. fel. Hb. Hampe'. The packet containing the specimen is labelled by Nylander 'Stictina fragillima Nyl. f. dissimilis Nyl. Australia'.

Morphology: Thallus very variable, orbicular to irregularly spreading, 5–12(–25) cm diam., loosely to closely attached centrally, margins ± free often ascending, terricolous, saxicolous or corticolous. *Lobes* very variable, ± linear-elongate to shallowly rounded, (1–)3–7(–12) mm wide, (1–)2–5(–10) cm long, branching subdichotomous to irregular, ± discrete at apices, discrete or contiguous from margins to centre, to complex-imbricate centrally, often ± canaliculate, sometimes divided into numerous, ± strap-like phyllidia. *Margins* entire, sinuous, smoothly rounded or ridged above, ± distinctly thickened below, sinuses rounded to acute, ± prominent, becoming isidiate and/or phyllidiate, without soredia or pseudocyphellae. *Upper surface* dark leaden-grey to blue-black at margins, paler centrally, with minute, white, marbled maculae when moist (× 10 lens), pale grey-blue, or glaucous-grey when dry, becoming cinnamon-brown on storage and often staining herbarium paper orange-red or brown, smooth or shallowly wrinkled, often with minute, pale buff or whitish, scattered to crowded papillae (× 10 lens), glossy to matt. *Isidia* marginal then laminal, simple, terete, 0·5–2·5(–3·5) mm tall, 0·1 mm diam., becoming densely crowded, coralloid branched and eventually flattened and ± phyllidiate. *Phyllidia* mainly marginal, constricted at base, simple, strap-like to palmate-squamiform. *Maculae* laminal, minute, marbled, scattered, irregular, pale buff or brown photobiont-free zones often present as often extensive blotches or patches. *Medulla* white. *Photobiont Nostoc. Lower surface* white to pale buff at margins, brownish centrally, glabrous, shining at margins, ± distinctly costate and tomentose centrally, tomentum short, velvety, often rather sparse, white, glistening. *Pseudocyphellae* white, widely scattered to numerous, flat, fleck-like, rather indistinct at margins, 0·01–0·1 mm diam., rarely to 0·3 mm diam., centrally, round to oval or sigmoid, decorticate area convex or plane, a thin margin often apparent, level with, or slightly projecting above, tomentum. *Apothecia* occasional to rare or absent, scattered, solitary to crowded (2–9 together), rounded to ± irregular-contorted through mutual pressure, marginal and laminal, sessile, constricted at base, 0·1–2·5 mm diam., shallowly concave to plane or undulate-convex, disc pale yellow-brown to dark red-brown, smooth to minutely granular, occasionally with central plugs of sterile tissue, epruinose, exciple pale whitish-buff to flesh-coloured, ± translucent when wet, scabrid-aereolate, ± crenulate at margins of disc.

Anatomy: Thallus 170–250 μm thick. *Upper cortex* 39–47 μm thick, pale straw-yellow, upper cells compressed, inner cells more loosely arranged, 6·5–18 μm diam. *Photobiont layer* 27–45 μm thick *photobiont Nostoc. Medulla* 73–110 μm, colourless, hyphae 5 μm diam. *Lower cortex* 27–34 μm thick, outermost row of cells yellow-brown to red-brown, cells 9–12 μm diam., inner rows of cells larger and thinner-walled, 11–15(–20) μm diam., more loosely arranged. *Tomental hairs* yellow-brown, slightly constricted at septa, 4·5–7 μm diam., 34–112 μm long, scattered, single. *Apothecia: Exciple* cellular, cells thick-walled, colourless to pale straw-yellow, 8–27 μm diam. *Hypothecium* 55–62 μm thick, pale yellow-brown to pale straw-yellow, not changing in K. *Thecium* colourless, 90–102 μm tall; *epithecium* yellow-brown to pale red-brown, unchanged in K, to 12 μm thick. *Asci* 77–95 × 11–15 μm. *Ascospores* pale yellow-brown, fusiform-ellipsoid, 1-3-septate, straight or slightly curved, apices rounded or pointed, 20·5–29·5 × 7–9 μm.

Chemistry: gyrophoric acid (tr.), 7β-acetoxyhopan-22-ol, hopane-7β 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: Pseudocyphellaria dissimilis is a highly variable australasian or, possibly palaeotropical, species having linear-elongate to shallowly rounded, subdichotomously to irregularly branched lobes, often ± canaliculate and with entire margins becoming isidiate or occasionally also phyllidiate. The upper surface is smooth or shallowly wrinkled, glossy or matt, minutely maculate and papillate (×10 lens), and with marginal and laminal isidia, and/or phyllidia (Fig. 55) Isidia are simple, ± terete at first and later may become coralloid-branched, or flattened and ± phyllidiate, though simple, terete isidia are most common. It has a white medulla, a blue-green photobiont, and a pale to brownish often ± costate lower surface with rather sparse, short, central tomentum and scattered, white, fleck-like pseudocyphellae. Apothecia are rare, sessile, with a pale, scabrid-areolate exciple. Spores are pale yellow-brown, 1-3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)], ± gyrophoric acid.

Variation: Pseudocyphellaria dissimilis is an extremely variable species having a highly plastic morphology, with lobes varying from narrow, ± strap-like with only a few marginal isidia and only 1-2-branched, to highly divided, imbricate, densely isidiate or phyllidiate structures. Isidia in *P. dissimilis* in the majority of cases are ± terete but occasionally terete isidia and ± flattened dorsiventral phyllidia occur on the same plant, which suggests a rather broad spectrum of variation in these structures in this species, possibly related to specific microclimate or microhabitat conditions. The diversity in lobe morphology parallels that seen in *P. multifida* and it seems likely that this latter taxon is the green-photobiont counterpart species of *P. dissimilis*.

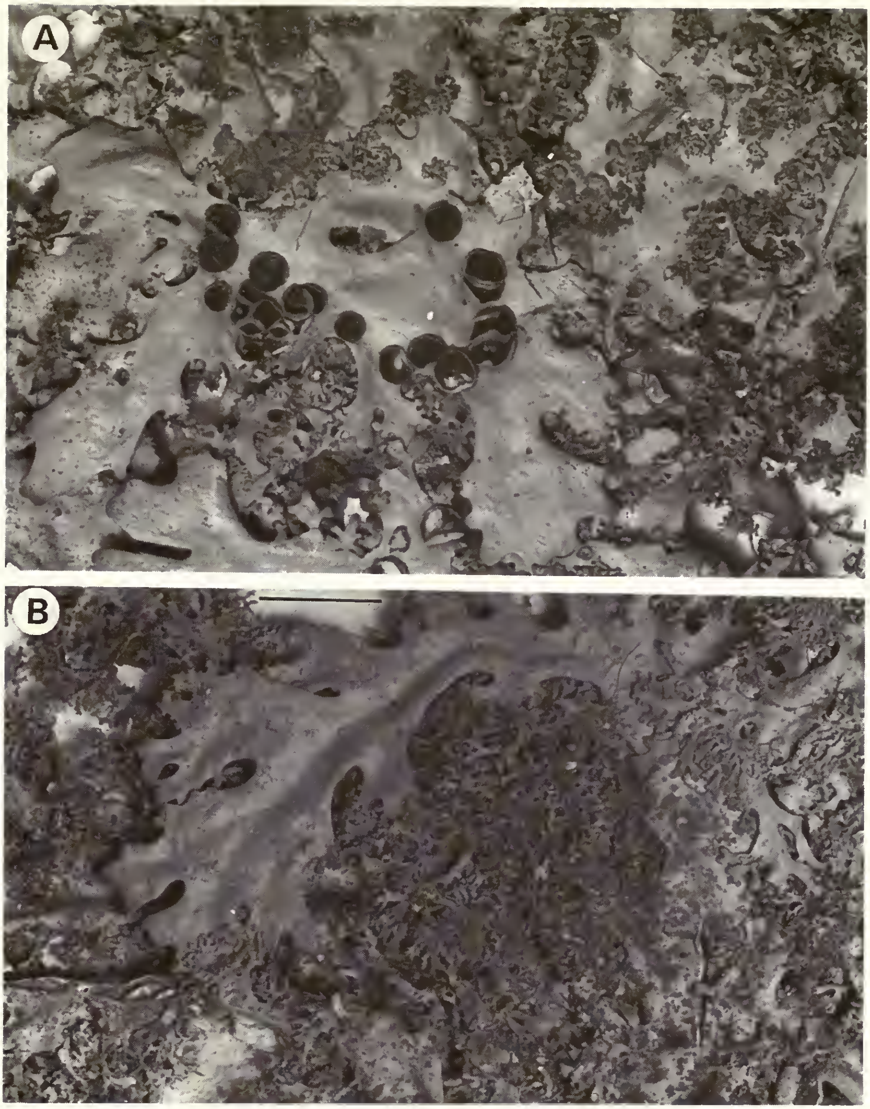

Fig. 55 *Pseudocyphellaria dissimilis*. New Zealand, *Helms* (W). A. Showing apothecia. B. Showing profuse development of phyllidia. Scale = 5 mm.

Photosymbiodemes of the two species are known from near the Lewis Pass in South Island, but are extremely rare.

Pseudocyphellaria dissimilis is distinct from *P. cinnamomea*, which is closely related, differing in the narrow, straplike, ± strongly canaliculate lobes with entire margins which are never isidiate or phyllidiate, and its lower surface is always distinctly costate-ridged. *Pseudocyphellaria fimbriatoides* is also similar to *P. dissimilis* but its phyllidia are noticeably pubescent and its lobes are broader, ± undulate, and shining, resembling *Peltigera*. An Australian-? palaeotropical species *P. insculpta* (not known from New Zealand) resembles *P. dissimilis* but has a distinctive punctate-impressed upper surface (reminiscent of *P. haywardiorum*, *P. junghuhniana*, *P. rigida*, and *P. sulphurea*) and very narrow sublinear lobes which are very richly divided and may even be ± phyllidiate but which are never furnished with terete isidia.

Dried specimens of *P. dissimilis* (and also *P. cinnamomea*) stain herbarium paper reddish brown after long storage.

Distribution: (Fig. 56) From North Auckland (lat. 35°S) to Wellington in North I., and from Nelson to Fiordland and eastwards from Marlborough to Invercargill in South I. Also in Stewart I., from Mt Anglem to Port Pegasus, mainly lowland, both coastal and inland, occasionally to ± subalpine, sea-level to 700 m.

Habitat ecology: Pseudocyphellaria dissimilis is tolerant of low light intensities and is the most common (often the sole) species of the genus to be found in deeply shaded habitats in New Zealand. Very often it is the only major lichen epiphyte in dark forest interiors, especially in North I. forests where it is very common, often in association with *Clathroporina exocha* and *Metus conglomeratus*. It grows readily on damp soil, amongst mosses or on rocks on the forest floor, on tree roots, and on tree trunks in moderate to dense shade, but is rare on twigs in these habitats. It prefers damp, cool, humid habitats and in these habitats it is an efficient fixer or atmospheric nitrogen (Green *et al.*, 1980). As such, it makes a significant contribution to the nitrogen balance of northern rain forests.

It is known from the following phorophytes: *Agathis australis*, *Ascarina lucida*, *Beilschmiedia taraire*, *B. tawa*, *Carpodetus serratus*, *Cordyline australis*, *Cyathodes*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *D. intermedium*, *Dysoxylum spectabile*, *Griselinia littoralis*, *Knightia excelsa*, *Melicytus ramiflorus*, *Metrosideros excelsa*, *M. lucida*, *Nothofagus fusca*, *Podocarpus hallii*, *P. totara*, *Prumnopitys ferruginea*, *Pseudopanax anomalus*, *P. arboreus*, *Pseudowintera colorata*, *Rhipogonum scandens*, *Rhopalostylis sapida*, *Sphaeropteris medullaris*, and *Weinmannia racemosa*.

Pseudocyphellaria dissimilis associates with the following lichens: *Calycidium cuneatum*, *Clathroporina exocha*, *Letogium azureum*, *L. cyanescens*, *Lobaria adscripta*, *L. retigera*, *L. scrobiculata*, *Metus conglomeratus*, *Nephroma cellulosum*, *N. plumbeum*, *N. helveticum*, *Normandina pulchella*, *Pannaria crenulata*, *P. immixta*, *Parmeliella nigrocincta*, *Peltigera dolichorhiza*, *Polychidium contortum*, *Pseudocyphellaria billardierei*, *P. colensoi*, *P. faveolata*, *P. glabra*, *P. fimbriatoides*, *P. homoeophylla*, *P. hookeri*, *P. multifida*, *P. murrayii*, *P. rufovirescens*, *Psoroma sphinctrinum*, *Sphaerophorus insignis*, *S. notatus*, *S. tener*, *Sticta caliginosa*, *S. filix*, *Sl. lacera*, and *S. subcaperata*.

Specimens examined: 205.

18. Pseudocyphellaria durietzii D. Galloway **Fig. 57**

in *Lichenologist* **15**: 142 (1983). Type: New Zealand, Stewart I., Lower Kopeka River, on *Coprosma foetidissima* roots on rata, in riverine rata-kamahi-totara-miro forest, *c.* 10 m, 12 February 1980, *C. D. Meurk* (CHR 375960! – holotype, BM! – isotype).

Morphology: Thallus rosette-forming to irregularly spreading, 10–15 cm diam., adnate centrally, rather loosely attached at margins, corticolous. *Lobes* subdichotomously to irregularly branching, 0·5–1·5 cm wide, 2–6 cm long, discrete or subimbricate at margins, often ± discrete or contiguous from margins to centre. *Margins* entire, occasionally slightly notched, shallowly sinuous, without projecting pseudocyphellae, not noticeably thickened below. *Upper surface* olive or yellowish green to fresh green when wet, pale olivaceous or grey-buff when dry, strongly reticulate-faveolate, ridges prominent, to 1 mm wide, smoothly rounded, furnished with minute, punctiform, red-brown pycnidia, faveolae prominent, deeply lacunose, 2–5 mm wide; smooth to very faintly wrinkled or pitted, matt or slightly shining, soredia, isidia, maculae, phyllidia, and pseudocyphellae absent. *Medulla* white. *Photobiont* green. *Lower surface* pale yellowish buff or whitish at margins, yellow-brown centrally, strongly wrinkled-bullate, glabrous in patches or with scattered tomentum, tomentum very thin, patchy, pale buff or yellow-brown. *Pseudocyphellae* common, scattered, minute, papillate, ± hemispherical, 0·1 mm diam. or less, decorticate area white, flat, minute, 0·03 mm diam. *Apothecia* marginal or submarginal, never laminal, 1–5(–8) mm diam., sessile to subpedicellate, pedicel best seen in young fruits, 0·5–1·5 mm wide, ± concave, margins inrolling and often obscuring disc, often also ± lacerate-striate or scalloped, without phyllidia, disc matt or shining to minutely granular, dark red-brown to black, epruinose, imperforate, exciple concolorous with thallus or suffused

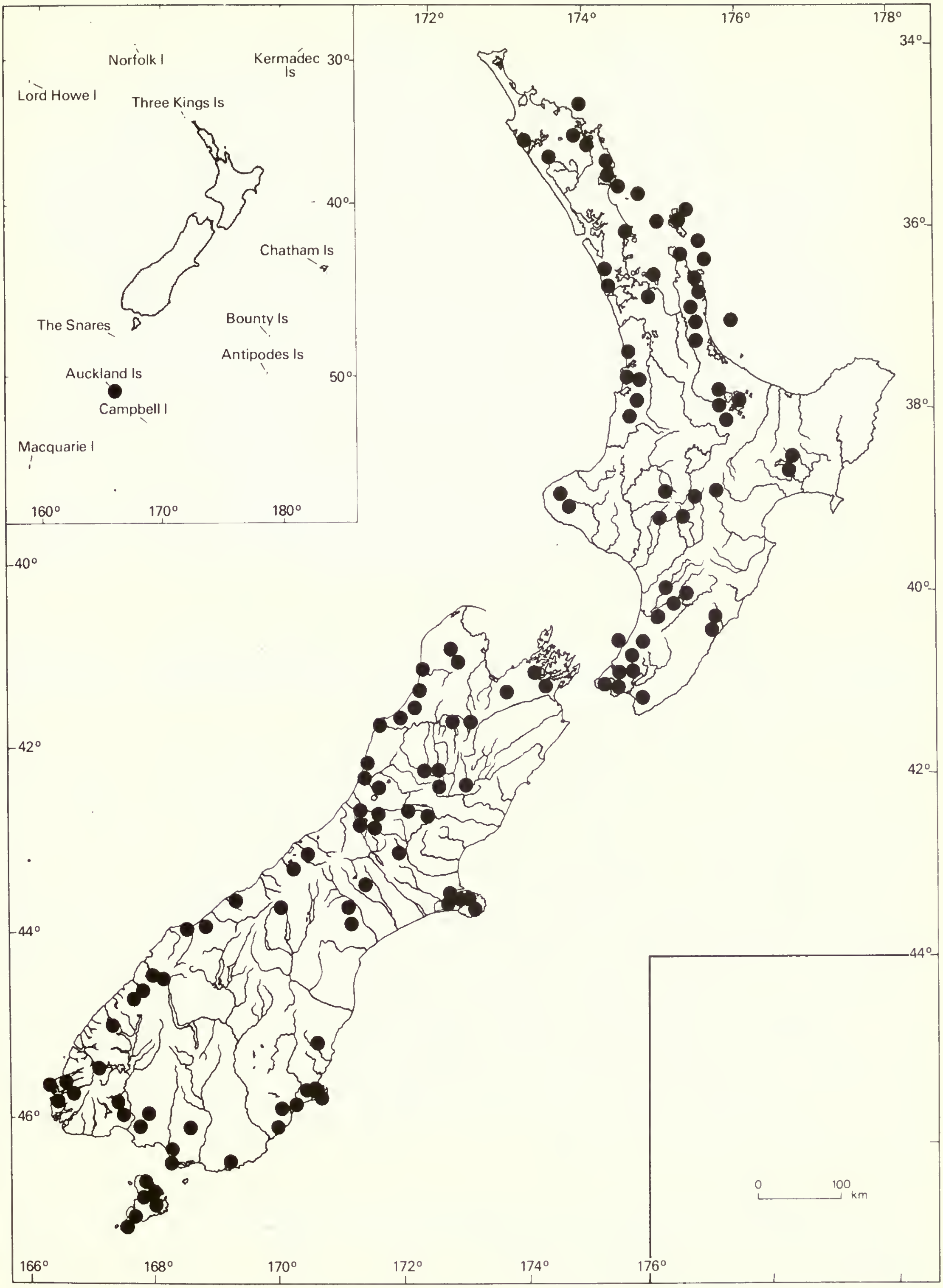
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Fig. 56 Distribution of *Pseudocyphellaria dissimilis*.

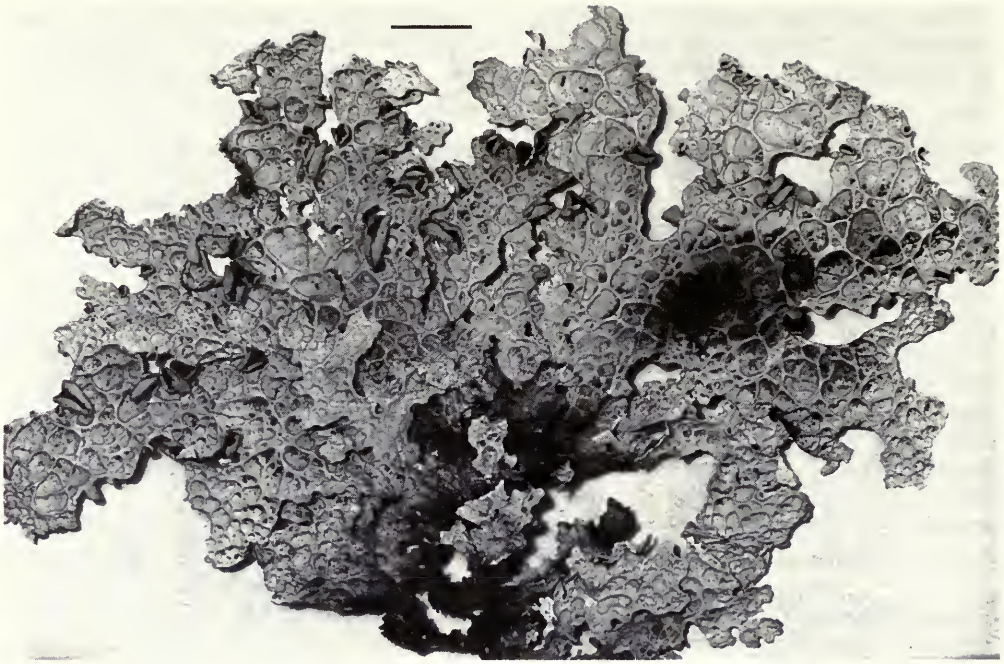


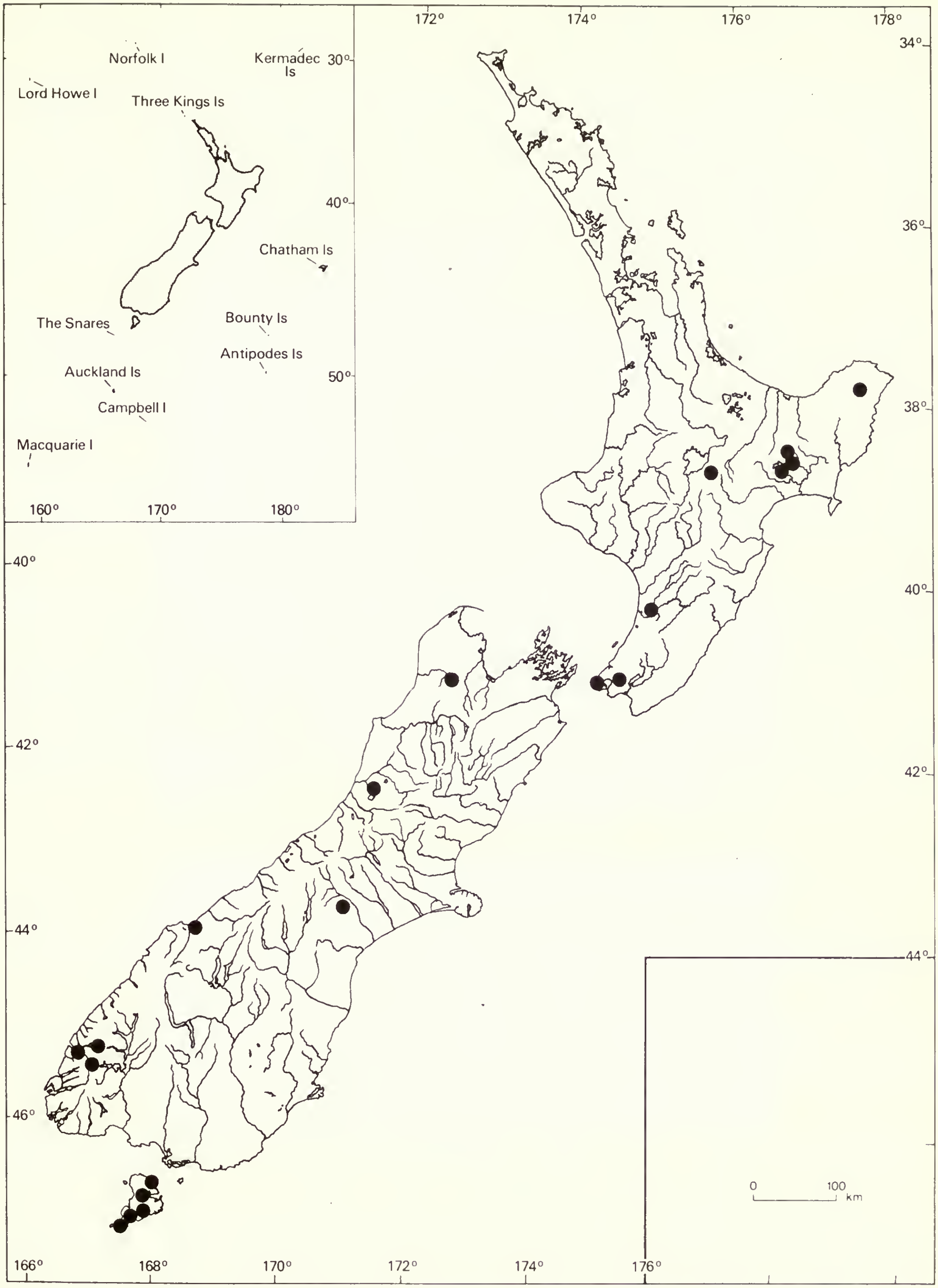
Fig. 57 *Pseudocyphellaria durietzii*. Holotype (CHR). Scale = 1 cm.

brownish at margins, smooth and shining at margins, ± minutely areolate to delicately pilose-scabrid towards pedicel, smooth or occasionally coarsely rugose-plicate towards base. *Pycnidia* common, mainly on reticulate ridges of upper surface, minute, papillate, apical ostiole red-brown to black. 0·2 mm diam., or less.

Anatomy: *Thallus* 110–150(–200) µm thick (360–600 µm thick at ridges). *Upper cortex* 18–23 (–27) µm thick, outer 7–9 µm, pale orange- or yellow-brown, cells stretched and compressed, inner 11–14 µm colourless, cells to 5 µm diam. *Photobiont layer* 11–22 µm thick, *photobiont* yellow-green, cells round to irregular, 3–5 µm diam. *Medulla* 27–110(–500 at ridges) µm thick, hyphae loosely interwoven, encrusted with granular crystals. *Lower cortex* 14–22 µm thick, colourless to pale straw, cells (3–5 rows), 4–5 µm diam. *Tomental hairs* sparse, pale straw, simple, septate, to 5 µm thick and 20–90(–140) µm long, in fascicles. *Pycnidia* ± hemispherical to oval, 170–210 µm diam. *Cephalodia* forming in medulla below photobiont layer and bursting through lower cortex, ovoid, 135–165 × 90 µm, *Nostoc* in a layer (35–45 µm thick) in uppermost part of structure. *Apothecia: Exciple* containing photobiont layer and medulla as in thallus, 35–45(–60) µm thick, cells pale straw, walls 2–3 µm thick, lumina very small, 2 µm or less, tissue rather irregular and ragged below, splitting off into irregular, ± pyramidal groups of cells. *Hypothecium* 35–45(–50) µm thick, dilute orange-brown, granular, opaque. *Thecium* colourless to pale straw, 70–90 µm tall; *epithecium* 7–11 µm thick, smoky grey-brown, turning vinous-purple in K, minutely granular. *Asci* 60–80 × 18–21 µm.*Ascospores* oval-ellipsoid with pointed ends, straight or slightly curved, brown, thickened 1-septate, septum variable 2-4·5 µm thick, narrower at maturity, 23–25 × 9–11 µm.

Chemistry: Methyl evernate, tenuiorin, methyl lecanorate, evernic (tr.) and gyrophoric acids, and four unidentified depsides, hopane-7β, 22-diol (tr.), hopane-6α, 7β, 22-triol, 7β-acetoxyphopane-αa, 22-diol (tr.), 6α-acetoxyhopane-7β, 22-diol, norstictic (tr.), stictic, hypostictic, cryptostictic, and constictic acids.

Pseudocyphellaria durietzii is named for G. Einar Du Rietz, formerly Professor of Ecological Botany and Director of the Växtbiologiska Institutionen, Uppsala University, who, with his first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42°
44°
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166°
168°
170°
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174°
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km

Fig. 58 Distribution of *Pseudocyphellaria durietzii*.

wife Greta Sernander-Du Rietz, first collected the species from rimu (*Dacrydium cupressinum*) bark in mixed rain forest on Seymour I., Doubtful Sound, Fiordland in 1927.

Distinguishing features: *Pseudocyphellaria durietzii* is an endemic species having ± dichotomously branching, linear-elongate to somewhat imbricate lobes with entire to ± crenulate margins. The upper surface is deeply and regularly reticulate-faveolate, without soredia, isidia, phyllidia, or pseudocyphellae. It has a white medulla, a green photobiont, and a pale buff, wrinkled-bullate, glabrous to scattered-tomentose lower surface. Apothecia marginal, subpedicellate, disc dark red-brown to black, exciple concolorous with thallus. Epithecium granular, smoky grey-brown, becoming vinous-purple in K. Spores brown, thickened 1-septate. It has a complex chemistry containing gyrophoric acid (cortex C+ red, fading fast) and other depsidones, hopane – 6α, 7β, 22-triol and metabolites of the stictic acid complex.

Variation: *Pseudocyphellaria durietzii* shows little morphological variation throughout its known range. It is related to *P. hookeri* (the two species have the same chemistry and epithecial colour reactions) but this species has a blue-green photobiont and a dark brown lower surface. In the Urewera National Park near the northern part of the range of *P. durietzii*, photosymbiodemes of two species are found. It is similar to *P. physciospora*, but this species has yellow pseudocyphelne and a different chemistry. See also Table 2 (p. 216).

Distribution: (Fig. 58) In North I., from Mt Hikurangi (lat. 37°55′S) and the Urewera National Park to Wellington, and from Nelson to Fiordland and Mt Peel (South Canterbury) in South I. Also in Stewart I., from the north coast to Port Pegasus and in Campbell I., mainly lowland to subalpine, sea level to 800 m.

Habitat ecology: *Pseudocyphellaria durietzii* is a species of lowland forest and scrub, favouring habitats of moderate shade, high humidity, and high rainfall. It is found in subalpine scrub on Mt Hikurangi, but in the Urewera National Park and on Stewart I., the two areas where it has until now been most commonly collected (scattered occurrences on the western mountains of North I., and from Nelson to Fiordland connect these two major population centres), it is found in open areas of ± lowland forest and/or scrub. It is an epiphyte of both bark and twigs of the following phorophytes: *Coprosma rhamnoides*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Ixerba brexioides*, *Metrosideros umbellata*, *Podocarpus totara*, *Prumnopitys ferruginea*, and *Weinmannia racemosa*.

Specimens examined: 30.

19. **Pseudocyphellaria episticta** (Nyl.) Vainio **Fig. 59**

in *Philipp. J. Sci.* C, **8**: 117 (1913). – *Sticta episticta* Nyl. in *Flora, Jena* **48**: 299 (1865). – *Lobaria episticta* (Nyl.) Trevisan, *Lichenotheca Veneta* exs. 75 (1869). Type: New Zealand, Otago, on trees, top of Saddlehill near Dunedin, 26 October 1861, *W. L. Lindsay* (H-NYL 33433! – holotype; E! – isotype).

The citation of the basionym (*Sticta episticta*) as Nylander, 1866: 248, in Galloway & James (1980: 298), and Galloway (1985*b*: 440) is incorrect. Even though Nylander (1866) gives a good description of the taxon in his discussion of Lindsay's Otago lichens, a valid description of the species appeared the previous year as shown above.

Morphology: *Thallus* rosette-forming to irregularly spreading, 5–10(–20) cm diam., closely attached centrally and to margins, apices slightly free and subascendent, corticolous, rarely saxicolous. *Lobes* linear-elongate, deeply indented, rather ragged, 0·5–1·5 cm diam., 2·5 cm long, apices and central parts complex-imbricate, folded. *Margins* lacerate-indented, ragged, rarely ± entire and shallowly rounded, usually sinuous and ± ascending, crisped, crenate to ± densely coralloid-phyllidiate, very slightly thickened below. *Upper surface* bright lettuce-green when moist, pale grey-green to fawnish or glaucous-yellow when dry, undulate, ± convex to subcanaliculate or plane, minutely wrinkled and/or pitted, not faveolate, matt or shining, rather coriaceous, without soredia, isidia or maculae, pseudocyphellate. *Pseudocyphellae* laminal,

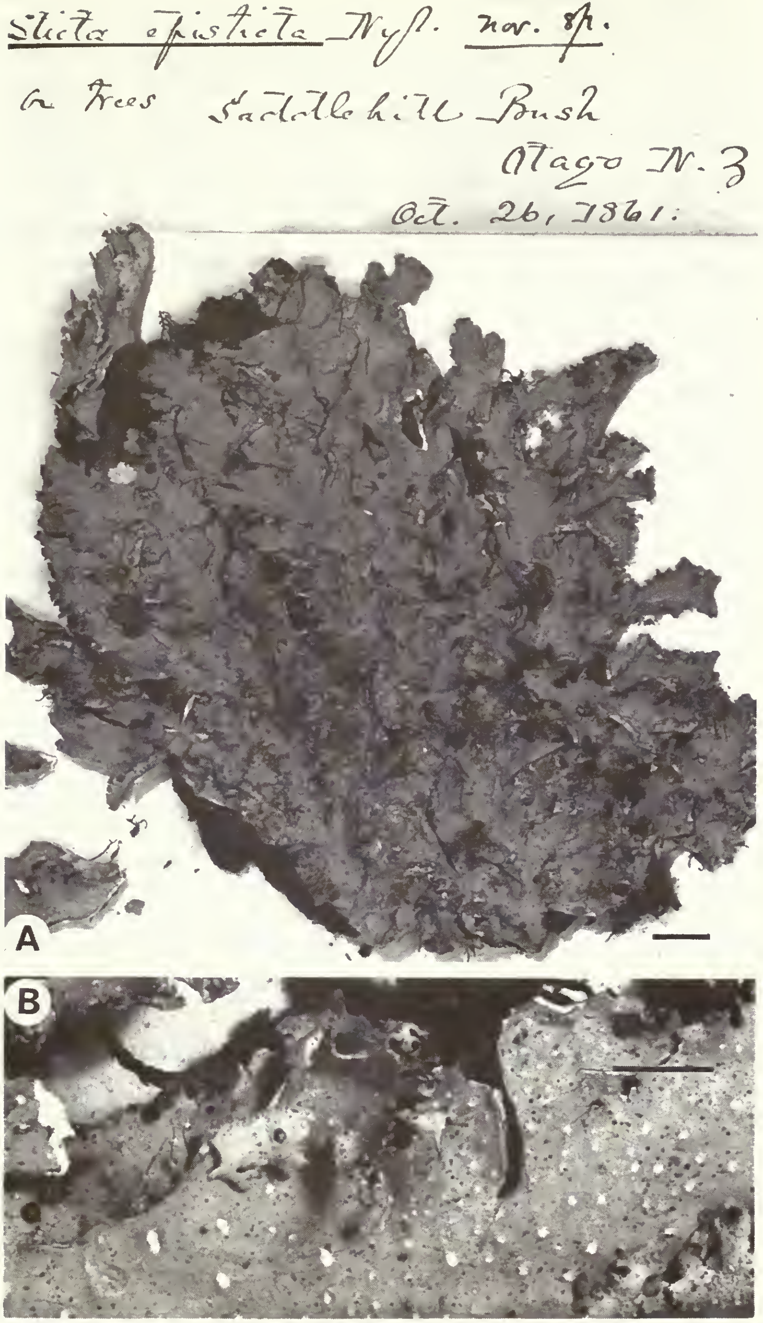

Sticta episticta Nyl. nov. sp.
on Trees Saddlehill Bush
Otago N.Z.
Oct. 26, 1861:
A
B

Fig. 59 *Pseudocyphellaria episticta*. Isotype of *Sticta episticta* (E). A. Scale = 1 cm. B. Scale = 2 mm.

scattered, white, punctiform, fleck-like to occasionally ± linear or effigurate, 0·05 mm diam. or less, rarely in older parts, regenerating phyllidia at margins. *Phyllidia* mainly marginal, simple at first and ± constricted at base, flattened, becoming coralloid-branched, 0·05–0·5 mm tall, often clustered, imbricate or forming extensive crusts, very occasionally on lamina and then rather scattered and irregular in appearance, not, or rarely, associated with pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* whitish to pale buff, darker centrally, tomentose from margins to centre or occasionally with a narrow, glabrous, slightly wrinkled, shining marginal zone, tomentum short, ± even, velvety to arachnoid-woolly, pale whitish-buff, glistening, to brownish or grey-brown. *Pseudocyphellae* white, sparse, occasional to rare, sunk in tomentum, or scattered, fleck-like at or near margins, decorticate area flat, 0·05–0·2 mm diam. *Apothecia* sessile, constricted at base, sparse to ± common (in favourable sites), solitary to crowded, laminal, 0·5–3 mm diam., round to irregular, constricted through mutual pressure, shallowly concave at first, plane, undulate at maturity, disc pale to dark red-brown, matt, minutely granular, epruinose, exciple pale whitish buff, translucent when moist, corrugate-scabrid, becoming ± irregularly phyllidiate in older fruits, margins often also ± excluded in older fruits, disc completely obscured by exciple in young, emergent fruits.

Anatomy: *Thallus* 230–275(–320) μm thick. *Upper cortex* 55–68 μm thick, uppermost 7–11 μm brown or yellow-brown, somewhat amorphous, remainder colourless to pale straw-yellow, cells 7–15 μm diam. *Photobiont layer* 34–45 μm thick, *photobiont* cells green, densely packed, 4·5–7 μm diam. *Medulla* 100–135(–220) μm thick, colourless, hyphae 3–4 μm diam. *Lower cortex* 36–45 μm thick, pale straw-yellow to yellow-brown, cells 4·5–15 μm diam. *Tomental hairs* colourless, simple, 5 μm thick, 60–110(–180) μm long, solitary or in small fascicles. *Apothecia: Exciple* colourless, 90 μm thick at margins, to 140 μm thick at base, outer surface splitting away into ragged clumps of cells (scabrosity), cells thick-walled, 4·5–13·5 μm diam. *Hypothecium* dilute yellow-brown, opaque, 45–64 μm thick. *Thecium* 90–100 μm tall, colourless to pale straw-yellow; *epithecium* red-brown, 18–22 μm thick, turning rose-pink in K and slowly dissolving; *paraphyses* strongly conglutinate, apices swollen, not moniliform. *Asci* 85–95 × 14–18 μm. *Ascspores* pale yellow-brown, fusiform, apices pointed, 1-3(rarely -7)-septate, slightly curved, cell contents distinctly vaculate, (27–)32–36·5(–41) × 7–9 μm.

Chemistry: 15α-acetoxy-22-hydroxyhopan-24-oic acid, 15α-22-dihydroxy-24-hopanoic acid.

Distinguishing features: *Pseudocyphellaria episticta* is an endemic species having linear-elongate, deeply indented, rather ragged lobes, with lacerate-crenate, cripsed margins which are ± densely coralloid-isidiate. The upper surface is pseudocyphellate, the pseudocyphellae occasionally associated at their margins with regenerating phyllidia, never with isidia. It has a white medulla, a green photobiont, and a pale buff or darker lower surface which is ± tomentose from margins to centre. Apothecia are sparse to common, the corrugate-scabrid exciple being irregularly phyllidiate at maturity. The epithecium is red-brown, turning rose-pink and dissolving in K, the spores pale yellow-brown, 1-3(rarely -7)-septate. It has two hopane acids present in the medulla (Ronaldson & Wilkins, 1978; Galloway *et al.*, 1983*b*; Galloway, 1985*b*).

Variation: *Pseudocyphellaria episticta* is a rather uniform species, though individual thalli may vary from ± neat rosettes to irregularly spreading colonies. Fertile specimens are reasonably common and in favourable sites apothecia are often densely crowded. It is most closely related to *P. wilkinsii* but has a differing chemistry, does not produce true isidia, and has a distinctive epithecial colour change in K. It is distinguished from *P. chloroleuca* by its tomentose lower surface, the different chemistry (its cortex is C–), and lack of true isidia. *P. multifida* lacks the laminal and marginal phyllidia, and the laminal pseudocyphellae characteristic of *P. episticta* and also has a different chemistry.

Distribution: (Fig. 60) North Auckland (lat. 36°S) to Cook Strait in North I., and spasmodically in South I., from Westland (Greymouth), Canterbury (Lewis Pass, Banks Peninsula, Mt Peel), and eastern Otago (Waikouaiti, Green Island, Saddle Hill, Lamb Hill, Flagstaff), mainly lowland and coastal, sea-level to 800 m.

Habitat ecology: *Pseudocyphellaria episticta* is found in lowland to montane forest in cool, moist, humid habitats of moderate illumination close to the forest margins. Mainly collected from tree trunks (not from twigs) it will also occasionally colonize coastal rocks and also rocks in tussock grassland. It is known from the following phorophytes: *Coprosma* spp., *Dacrycarpus dacrydioides*, *Dysoxylum spectabile*, *Griselinia littoralis*, *Knightia excelsa*, *Leptospermum*

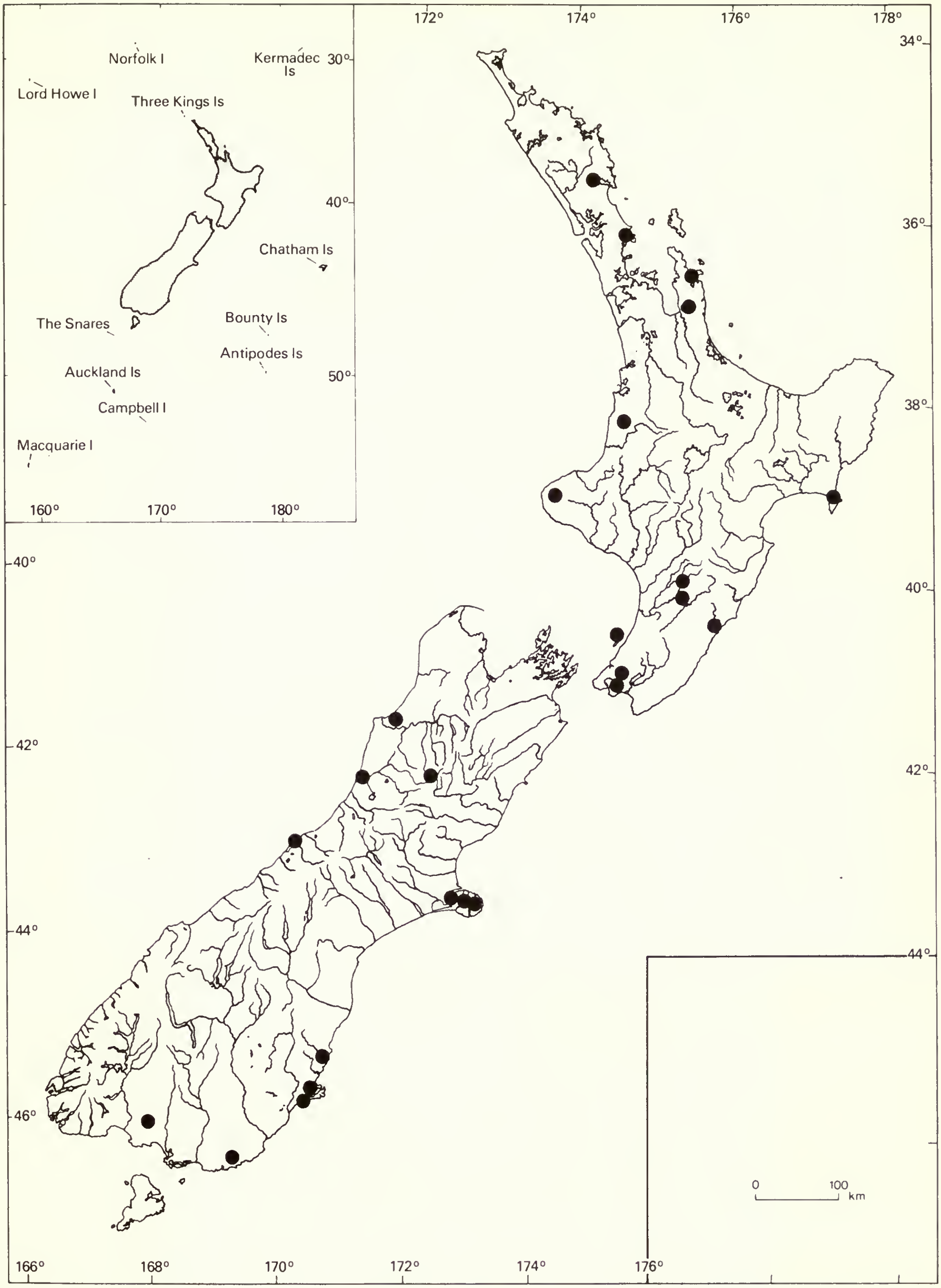

Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
40°
50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 60 Distribution of *Pseudocyphellaria episticta*.

scoparium, *Nothofagus menziesii*, *Podocarpus hallii*, and *P. totara*. It associates with the following lichens: *Lobaria adscripta*, *Parmelia tenuirima*, *Parmelia testacea*, *Pseudocyphellaria coriacea*. *P. pickeringii*, *P. rufovirescens*, *Sticta filix*, *S. latifrons*, and *S. subcaperata*.

Specimens examined: 70.

20. Pseudocyphellaria faveolata (Delise) Malme — Figs 61, 62

in *Bih. K. svenska Vetensk.-Akad. Handl.* **25**(3/6): 23 (1899). – *Sticta faveolata* Delise in *Mém. Soc. linn. Normandie* **2**: 102 (1825). – *Stictina faveolata* (Delise) Nyl., *Syn. Meth. Lich.* 1(2): 337 (1860). – *Cyanisticta faveolata* (Delise) Räsänen in *Annls Bot. Soc. zool.-bot. fenn. Vanamo* **2**(1): 42 (1932). Type: Straits of Magellan, sine collectoribus nomine (BM! – lectotype) [see Galloway *et al.* (1983*b*: 140); Galloway & James (1986)].

Sticta cellulifera J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 647 (1844). – *Crocodia cellulifera* (J. D. Hook. & Taylor) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Diphanosticta cellulifera* (J. D. Hook. & Taylor) Clements, *Gen. fung.*: 175 (1909). – *Pseudocyphellaria cellulifera* (J. D. Hook. & Taylor) Gyelnik in *Feddes Reprium Spec. nov. veg.* **29**: 2 (1931). – *Sticta foveolata* var. *cellulifera* (J. D. Hook. & Taylor) Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 278 (1855). – *S. fossulata* var. *cellulifera* (J. D. Hook. & Taylor) Nyl., *Syn. meth. lich.* **1**(2): 364 (1860). – *S. billardierei*

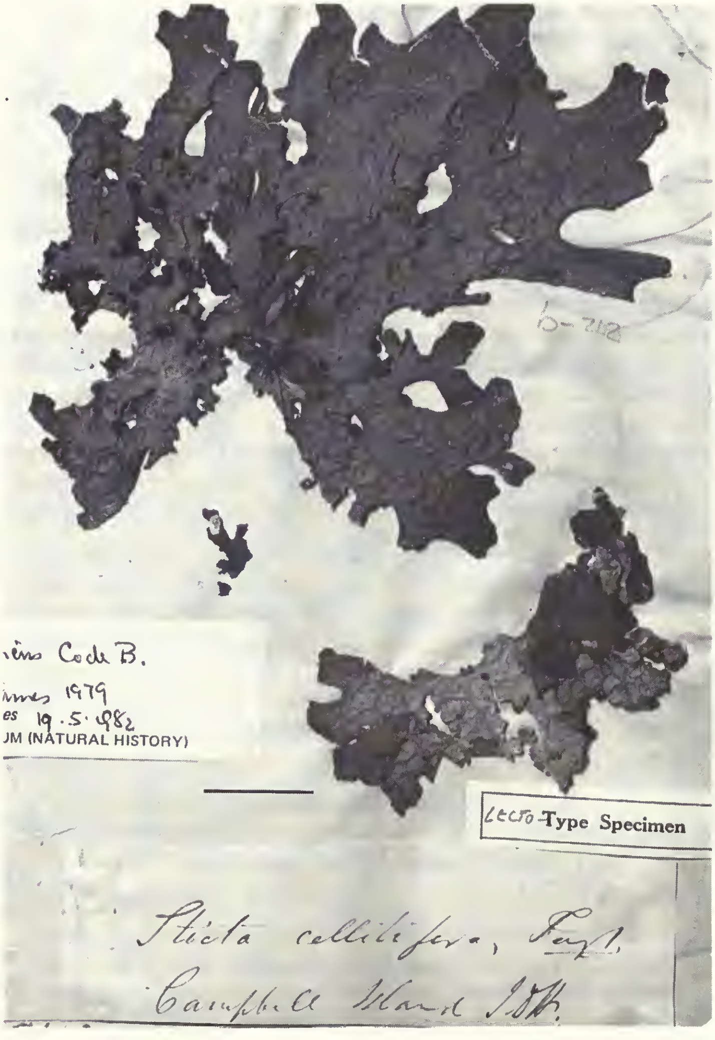


Fig. 61 *Pseudocyphellaria faveolata*. Lectotype of *Sticta cellulifera* (BM). Scale = 2 cm.

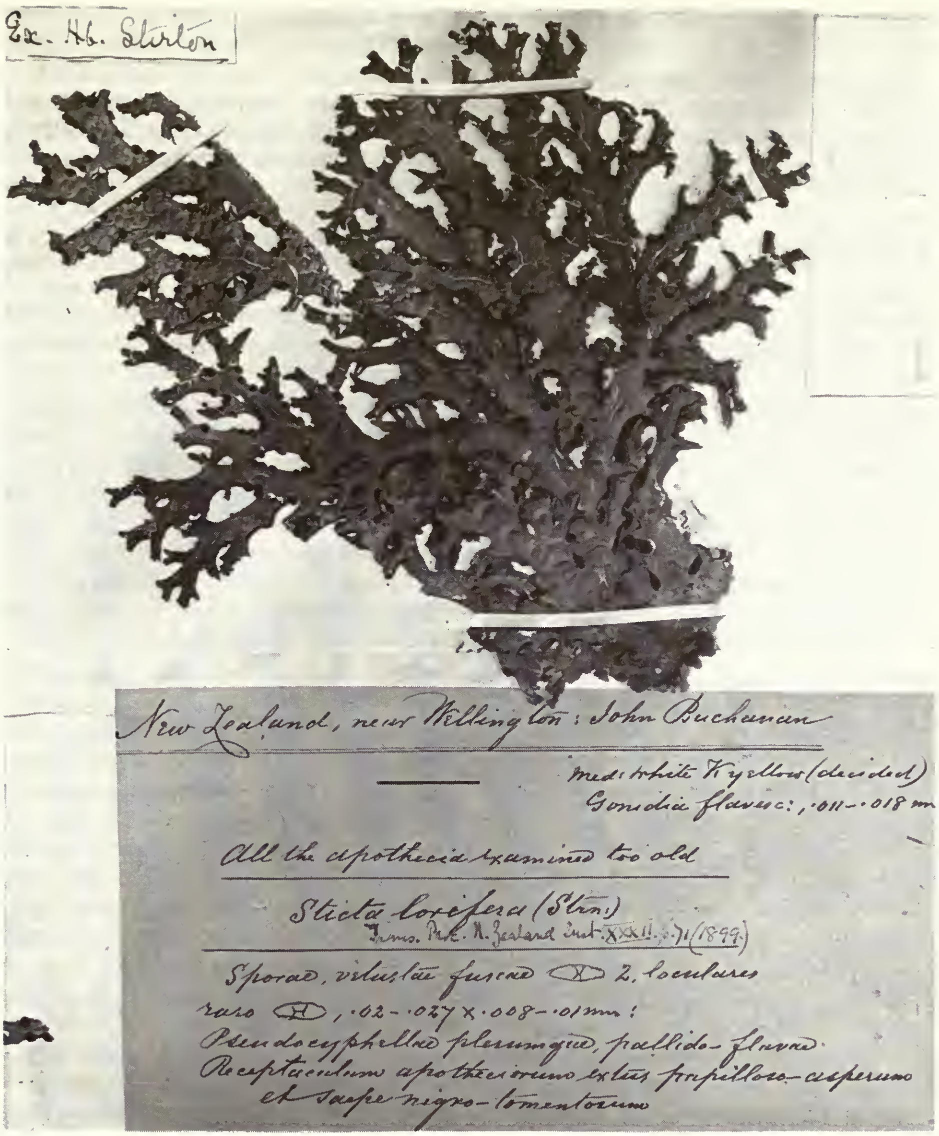

Ex. Hb. Stirton
New Zealand, near Wellington: John Buchanan
Med: white & yellow (decided)
Gonidia flavesc: ; ·011–·018 mm
All the apothecia examined too old
Sticta lorifera (Stirt.)
Trans. Proc. N. Zealand Inst. XXXII. p. 71 (1899)
Sporae, vetustae fuscae 2, loculares
raro , ·02–·027 × ·008–·01 mm:
Pseudocyphellae plerumque, pallido-flavae.
Receptaculum apotheciorum extus papilloso-asperum
et saepe nigro-tomentosum

Fig. 62 *Pseudocyphellaria faveolata*. Lectotype of *Sticta lorifera* (BM). Scale = 2 cm.

var. *cellulifera* (J. D. Hook. & Taylor) Müll. Arg. in *Flora, Jena* **71**: 135 (1888). – *Lobaria billardierei* var. *cellulifera* (J. D. Hook. & Taylor) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21**(3/13): 41 (1896). Type: Campbell Island, *J. D. Hooker* (BM! – lectotype) [see note 1]. Fig. 61

Sticta lorifera Stirton in *Trans. N.Z. Inst.* **32**: 71 (1900). Type. New Zealand, near Wellington, *J. Buchanan* (BM! – lectotype; BM! – isotype). Fig. 62

Sticta elatior Stirton in *Trans. N.Z. Inst.* **32**: 73 (1900). Type: New Zealand, near Wellington, *J. Buchanan* (BM! – lectotype).

Sticta condensata Zahlbr. in *Denkschr. Akad. Wiss, Wien math.-naturwiss. Kl.* **104**: 280 (1941). – *Pseudocyphellaria condensata* (Zahlbr.) D. Galloway & P. James in *Lichenologist* **12**: 294 (1980). Type: New Zealand, Southland, Riverton Bush, on rotten log, *J. S. Thomson* ZA 541 (W! – holotype; BM! CHR 317808! – isotypes) [see Galloway, 1986*b*].

In a preliminary account of the confused nomenclature of this species and its synonyms (Galloway & James, 1980: 298) several taxa were recorded incorrectly as synonyms and are now placed elsewhere viz., *Sticta fossulata* [= *P. billardierei*]; *S. flotowiana* [= *P. billardierei*]; *S. linearis* [= *P. billardierei*]; *S. impressa* [= *P. carpoloma*]; *S. physciospora* [= *P. physciospora*].

Note 1: *Sticta cellulifera* J. D. Hook. & Taylor
Thomas Taylor based his name *Sticta cellulifera* on broadly lobed, deeply faveolate specimens from Campbell Island, the Auckland Islands, and New Zealand. Material annotated *S. cellulifera* by Taylor in the BM is referable to *Pseudocyphellaria faveolata*, the specimens containing the characteristic marker compound for this species, physciosporin. Of the three specimens (all collected by J. D. Hooker) annotated *S. cellulifera* by Taylor in his own herbarium (FH), one from Campbell I. is *P. faveolata*, one from the Auckland Is is referable to *P. billardierei*, and the specimen from New Zealand is referable to *P. hookeri*. Hooker's interpretation of *S. cellulifera* (Taylor & Hooker, 1845: 198) records yellow pseudocyphellae in the material discussed and refers to *P. physciospora* (see under that species), while Babington (1855: 278) made *S. cellulifera* a variety of *S. foveolata* [sic]. Fitch's illustration (plate CXXIV in Babington, 1855) shows pseudocyphellae strongly reminiscent of those of *P. faveolata*, and the deeply faveolate, broadly lobed form of this species.

Morphology: Thallus ± orbicular to spreading, often forming extensive entangled clones, loosely attached centrally, margins ± free, 5–15(25) cm diam., corticolous. *Lobes* linear-elongate, very variable in width, 20–40 mm wide at centre, 2–15 mm wide towards apices, 1–5(–10) cm long, ± discrete or contiguous to subimbricate at margins, complex-imbricate centrally, broad and somewhat rounded or blunt at apices, with branching, rather irregular or rather narrow and ± subdichotomously branching with apices ± furcate. *Margins* entire, shallowly sinuous or scalloped, suffused brownish at apices, slightly to markedly thickened above, with prominent, raised, conical-verrucose, white pseudocyphellae, rarely with irregularly coralloid isidia or lobules, sometimes ragged-uneven and ± subascendent. *Upper surface* bright lettuce-green to olive-green, suffused red-brown at apices when wet, pale olivaceous, buff, to dark green or green-black or olivaceous-brown when dry, coriaceous, matt or shining, rather waxy, strongly reticulate-faveolate, ridges mainly smoothly rounded, 0·1–1 mm wide, often copiously wrinkled-plicate, often with numerous pycnidia or pycnidial cavities arranged along ridges, faveolae very variable, shallow to deep, without isidia, maculae, pseudocyphellae or soredia, occasionally phyllidia develop at margins in response to insect damage. *Medulla* white. *Photobiont* green. *Lower surface* sometimes with a narrow, glabrous, wrinkled marginal zone at lobe apices, ± densely and uniformly tomentose to margins in older lobes, tomentum felted, brown or black, rarely pale buff or whitish. *Pseudocyphellae* conical-verruciform, raised above tomentum or slightly sunken below tomentum, numerous, prominent, 0·1–1 mm diam., with a conspicuous, inflated, smooth, fawn or buff to dark brown-black, waxy margin, decorticate area white, flat or slightly excavate. *Apothecia* mainly marginal or submarginal, rarely laminal, most commonly towards lobe apices, 1–4(–6) mm diam., shallowly concave at first, becoming plane to shallowly convex-undulate at maturity, subpedicellate, disc matt to slightly roughened, pale to dark red-brown when wet, black when dry, white-pruinose when young, epruinose at maturity, exciple whitish-arachnoid-scabrid at first and then completely obscuring disc, remaining for a time as a whitish to buff or pale red-brown, ragged-arachnoid margin, becoming excluded in mature fruits, buff-brown or whitish-arachnoid-scabrid below disc. *Pycnidia* occasional to frequent, mainly on reticulate ridges or scattered on floors of faveolae, minute, ± punctiform to hemispherical, to 0·5 mm diam., often completely eroded leaving rows of shallow pits along ridges, ostiole red-brown to black.

Anatomy: Thallus 180–250 (–600 at ridges and pycnidia) μm thick. *Upper cortex* 25–36 μm thick, outer zone (7–11 μm) dilute yellow-brown, of ± necrotic or tightly compressed cells, layer abutting photobiont zone colourless, cells 4·5–7 μm diam. *Photobiont layer* 35–45(–55) μm thick, *photobiont* green, cells round to irregular, 4·5–9 μm diam., chloroplast occupying most of cell. *Medulla* 70–150(–400) μm thick, colourless, of loosely interwoven hyphae to 4·5 μm diam., covered with small, granular crystals. *Lower cortex* 35 μm thick, comprising 4–5 rows of cells, similar in size and structure to those of upper cortex, outermost layer pale yellow-brown, inner zone colourless. *Tomental hairs* 4·5–7 μm thick, septate, simple, pale straw to red-brown, densely conglutinate in fascicles, 90–150(–250) μm long. *Apothecia: Exciple* colourless, cellular, 45 μm thick at margins, 90–100 μm thick below disc, of parallel, anticlinally arranged hyphae, cells 4·5–9 × 0·5–2·5 µm. *Hypothecium* 65–90(–112) µm thick, dense, opaque, upper parts orange-brown, lower half olive-brown to dark brown, ± granular. *Thecium* hyaline to pale straw, or dilute yellow-brown, rather granular, 100–120(–135) µm tall (lower parts occasionally greenish in K); *epithecium* dark grey-brown or olivaceous brown, 11–13·5 µm thick, turning vinous-purple in K. *Asci* 75–90 × 15–20 µm. *Ascospores* smoky grey to brown, oval-ellipsoid, apices pointed, thickened, 1-septate at first then 3-septate, septum 2·5–7 µm thick, 25–35 × 9–11 µm.

Chemistry: Methyl virensate, physciosporin, hopane-6α, 7β, 22-triol, stictic, norstictic (tr.), cryptostictic, and constictic acids [Code B of Wilkins & James (1979)].

Distinguishing features: *Pseudocyphellaria faveolata* is an austral species having linear-elongate, narrow to broad lobes, dichotomously to irregularly branched, apices divergent, blunt or acute, margins entire, thickened, with prominent, raised, verruciform, white pseudocyphellae, rarely also irregularly lobulate or isidiate (response to insect damage?). The upper surface coriaceous, waxy, reticulate-faveolate, without isidia, maculae, phyllidia, pseudocyphellae or soredia. It has a white medulla, a green photobiont, and a dark brown to black, often thickly tomentose lower surface, with scattered white or creamish, verruciform pseudocyphellae. Apothecia are marginal, subpedicellate, the disc dark red-brown to black, often white-pruinose when young, exciple whitish or buff-brown, arachnoid-scabrid, obscuring disc at first. Epithecium dark grey-brown, turning vinous-purple in K. Spores grey-brown, thickened 1-septate to 3-septate. It has a complex chemistry containing physciosporin and stictic acid metabolites [Code B of Wilkins & James (1979)].

Variation: *Pseudocyphellaria faveolata* is a widespread and very polymorphic lichen. Lowland forms tend to be narrow-lobed (Fig. 66) and ± regularly dichotomously branching, whereas subalpine forms close to tree-line, and in southern Stewart I., and the subantarctic islands (Auckland and Campbell Is) have broader, less regularly divided lobes (Fig. 65). The tomentum of the lower surface also varies from a thick, dense, dark matt from margins to centre, to a more open-textured covering mainly at centre leaving a conspicuous glabrous zone at the margins. Thalli exposed to full sun or to high light intensities especially at forest margins, or in open scrub communities, are noticeably darkened, either suffused brownish or even totally blackened. Shade forms on the other hand are without cortical darkening.

In the northern part of its range, *P. faveolata* in many habitats appears to be replaced by *P. carpoloma*, a superficially similar species but with vivid yellow pseudocyphellae below and a different chemistry [Code D of Wilkins & James (1979)], and lacking physciosporin. *P. faveolata* is distinguished from *P. rufovirescens* which has entire lobe margins without projecting pseudocyphellae, a pale, glabrous lower surface, red-brown marginal apothecia which are never pruinose, epithecial pigments giving no reaction in K, and a different chemistry [Code A of Wilkins & James (1979)]; and from *P. billardierei* which also has entire margins without pseudocyphellae, a sparse dark tomentum on the lower surface, marginal black, epruinose apothecia, epithecial pigments which turn green-black in K, and a different chemistry deficient in physciosporin [Code B of Wilkins & James (1979)]. *Pseudocyphellaria physciospora*, although similar in many respects to broad-lobed, subantarctic forms of *P. faveolata*, is distinguished from it in the entire lobe margins which lack pseudocyphellae, the minute yellow pseudocyphellae on the lower surface, and the ± stripitate, epruinose fruits which have a subdenticulate margin. The chemistry is also distinctive, lacking physciosporin, and containing tenuiorin, several triterpenoids not present in *P. faveolata*, plus norstictic and salazinic acids. See also Table 2 (p. 216).

Distribution: (Fig. 63) Throughout from lat. 35°S in North Auckland, though more commonly collected from lat. 38°S southwards in both main islands, also in Stewart I., the Snares, the Auckland, and Campbell Is; sea-level to 1200 m.

Habitat ecology: *Pseudocyphellaria faveolata* is a polymorphic, wide-ranging species occupying many habitat niches from windswept coastal scrub, lowland coastal forest, beech forest,

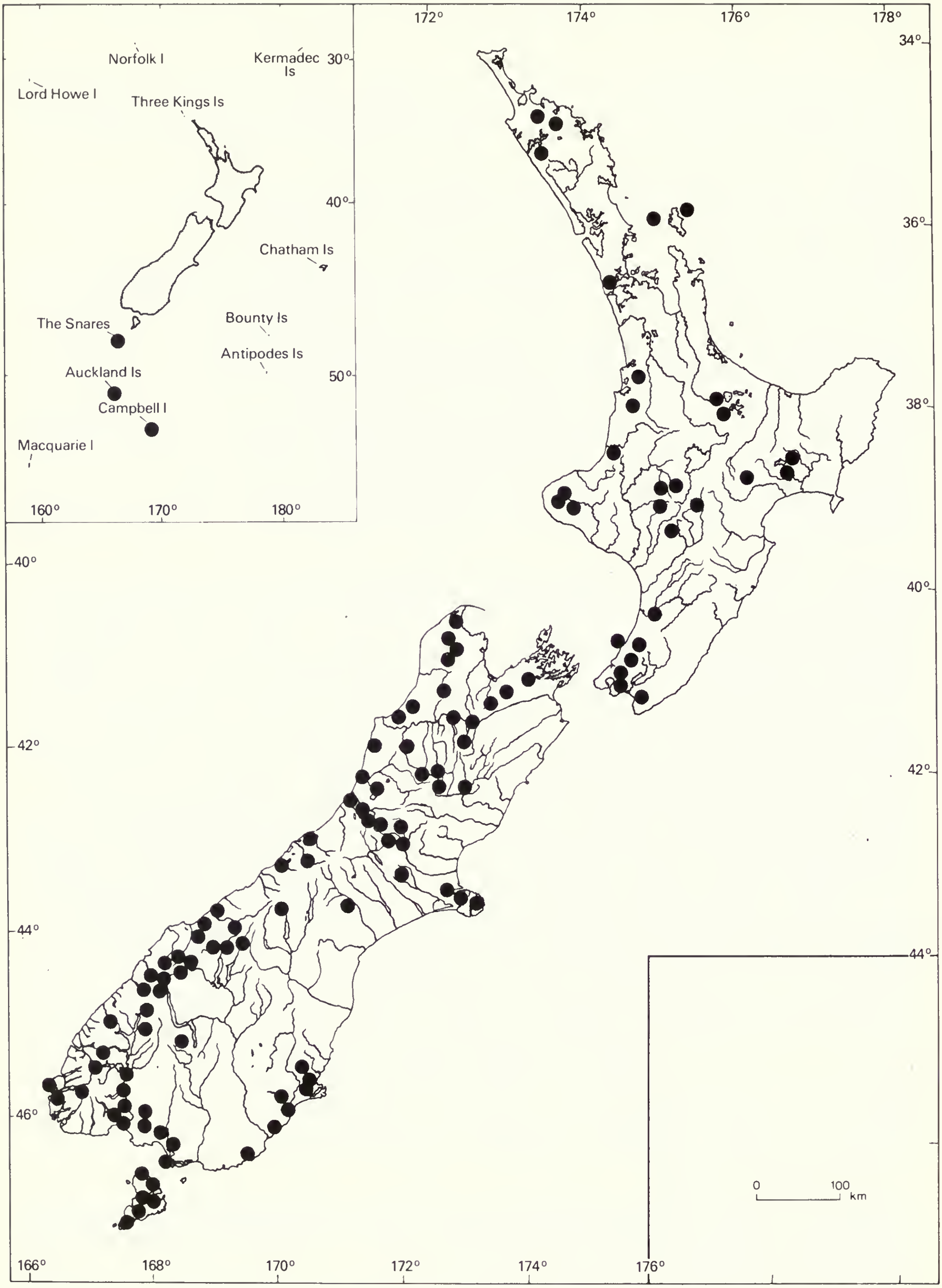

Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
40°
50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 63 Distribution of *Pseudocyphellaria faveolata*.

mixed beech-podocarp forest, subalpine scrub close to or above tree-line, to successional vegetation in altered sites. It is common on both bark and twigs, being especially well-developed in open forest habitats (close to margins of standing forest) in high-rainfall areas, and is more commonly collected from southern and western localities (Fig. 67). It is a moderately photophilous species and does not tolerate deep shade. It appears to be an obligate epiphyte and is not known from rocks or soil although it will attach to ferns. It is known from the following phorophytes: *Coprosma propinqua*, *C. pseudocuneata*, *Dacrydium cupressinum*, *Dracophyllum filifolium*, *D. longifolium*, *Griselinia littoralis*, *Ixerba brexioides*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros robusta*, *Myrsine divaricata*, *Myrtus obcordata*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Olearia colensoi*, *Pennantia corymbosa*, *Phyllocladus trichomanoides*, *Podocarpus hallii*, *P. nivalis*, *P. totara*, *Pseudopanax simplex*, *Pseudowintera colorata*, *Senecio eleagnifolius*, *S. reinoldii*, *Weinmannia racemosa*, and *W. silvicola*.

Specimens examined: 180.

21. **Pseudocyphellaria fimbriata** D. Galloway & P. James **Fig. 64**

in *Lichenologist* **15**: 142 (1983). Type: New Zealand, South I., Nelson, Lake Rotoiti (Nelson Lakes National Park), Peninsula, on bark of *Nothofagus menziesii*, 28 February 1980, *D. J. Galloway* (CHR 381021! – holotype, BM! – isotype).

Pseudocyphellaria hamata D. Galloway & P. James in *NZ Jl Bot.* **16**: 521 (1978), nom. nud. (Art. 32.1).

Morphology: *Thallus* orbicular to irregularly spreading, 6–12(–25) cm diam., loosely attached centrally, margins and apices free and ± ascending, corticolous and occasionally terricolous (among tussock bases). *Lobes* irregularly to complexly dissected, elongate-laciniate and ± contiguous or discrete from margins to centre, to very richly and complexly divided-imbricate, branching subdichotomous to very irregular, sinuses well-defined, semicircular, ± plane towards apices, becoming ± canaliculate centrally. *Margins* entire in parts to richly dissected, becoming copiously phyllidiate, often ascending, ± white-tomentose, tomentum short, glistening, with white, scattered pseudocyphellae or tomentum of lower surface visible. *Upper surface* bright lettuce-green to glaucous olive-green, suffused red-brown at apices when moist, pale greyish yellow to brownish or red-brown when dry, coriaceous, plane or ± canaliculate centrally or weakly wrinkled in parts, minutely scabrid-areolate (× 10 lens), without soredia, isidia, maculae or pseudocyphellae. *Phyllidia* mainly marginal, rarely laminal (and then regenerating from damaged cortex), fragile, flattened, dorsiventral, rarely simple, furcate to palmately divided to complex-imbricate to ± coralloid, 0·5–2·5 mm tall, margins glistening, delicately white, pubescent, lower surface with minute, white pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* whitish or pale buff, in a narrow marginal zone, pale red-brown to dark-brown or black centrally, tomentose from margins to centre, or with a narrow, ± glabrous, marginal zone, tomentum short, velvety at margins, thick, woolly centrally, pale red-brown marginally, dark-brown to black centrally. *Pseudocyphellae* white, conspicuous, numerous, 0·05–1(–2) mm diam., round to irregular, minute, flecklike at margins, larger, prominent centrally, decorticate area brilliant white, shallowly to deeply concave, margins narrow, slightly raised, inapparent. *Pycnidia* sparse to frequent, scattered, laminal, minute, punctate-depressed, ostiole red-brown. *Apothecia* sessile, constricted at base to subpedicellate, sparse, when present often towards lobe apices, marginal or submarginal, 1–3(–4) mm diam., concave to plane, round to slightly irregular, sinuous, margins pale whitish buff, disc pale to dark red-brown, smooth, matt or shining, epruinose, exciple pale whitish buff to red-brown, translucent when moist, coarsely verrucose-areolate, occasionally patchily tomentose, well-developed in young fruits and then often ± obscuring disc.

Anatomy: *Thallus* 180–275(–325) µm thick. *Upper cortex* 45–57(–68) µm thick, upper 18–27 µm pale straw-yellow, cells compressed, flattened, upper surface very uneven-irregular, remaining cells colourless, loosely arranged, 4·5–15(–20) µm diam. *Photobiont layer* 34–45 µm thick, *photobiont* green, cells rounded, 8–13·5 µm diam., chloroplast not filling whole of cell,

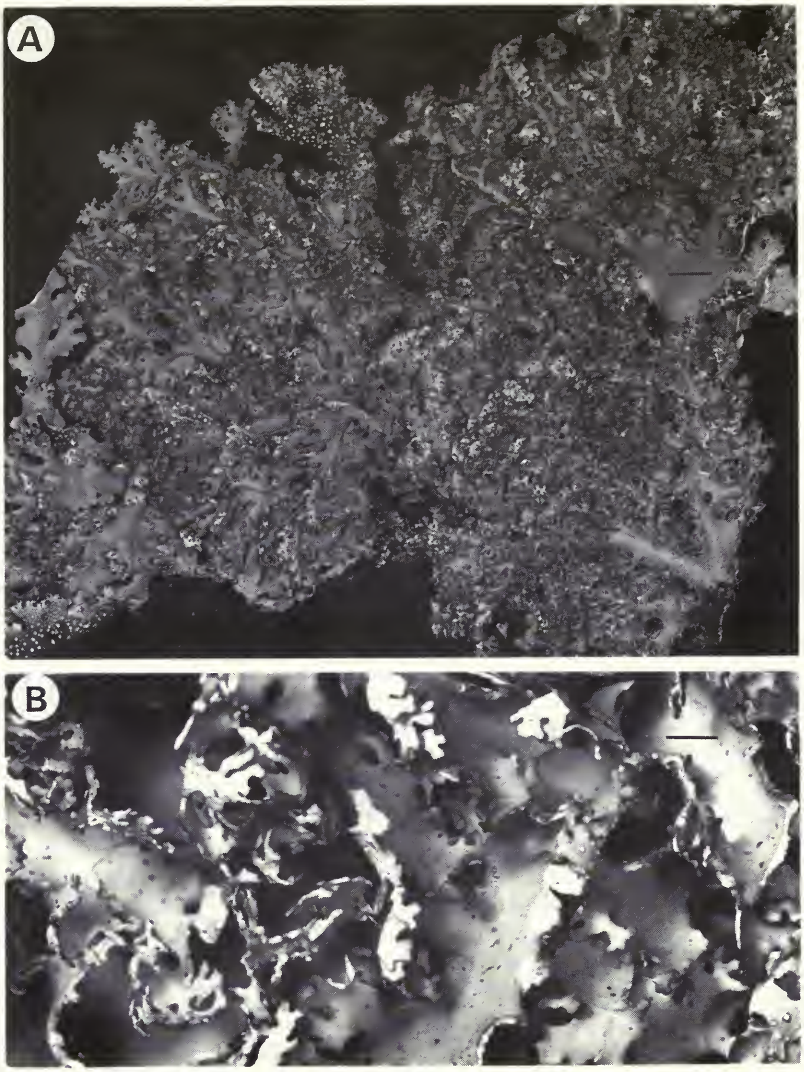


Fig. 64 *Pseudocyphellaria fimbriata*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 1 mm.

?*Dictyochloropsis*. *Medulla* 90–140(–185) µm thick, hyphae 4–5 µm diam. *Lower cortex* 28–34 µm thick, outer 7–10 µm dark red-brown, remainder pale straw-yellow, cells thick-walled, 4·5–9 µm diam. *Tomental hairs* colourless to pale red-brown, single or in fascicles 4–5 µm diam., 30–140 µm long. *Apothecia: Exciple* colourless, 110–200 µm thick, in ragged, pyramidal clusters at margins, cells thick-walled, 4·5–11(–15) µm diam. *Hypothecium* 45–58 µm thick, dilute yellow-brown, opaque, overlying a compact, colourless (greenish blue on addition of K), ± periclinal layer 30–45 µm which merges into the medulla proper. *Thecium* dilute yellow-brown 130–145 µm tall, with conspicuous oil droplets or granules investing paraphyses, colour dissolving in K or becoming ± greenish in parts; *epithecium* not apparent, concolorous with thecium. *Asci* 95–102 × 11–14 µm. *Ascospores* pale yellow-brown, broadly ellipsoid, apices rounded or pointed, 3-septate at maturity, locules irregularly vacuolate, 25–32 × 9 × 11 µm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria fimbriata* is an endemic species having elongate-laciniate, complexly dissected lobes with conspicuously phyllidiate margins (Fig. 64B). The

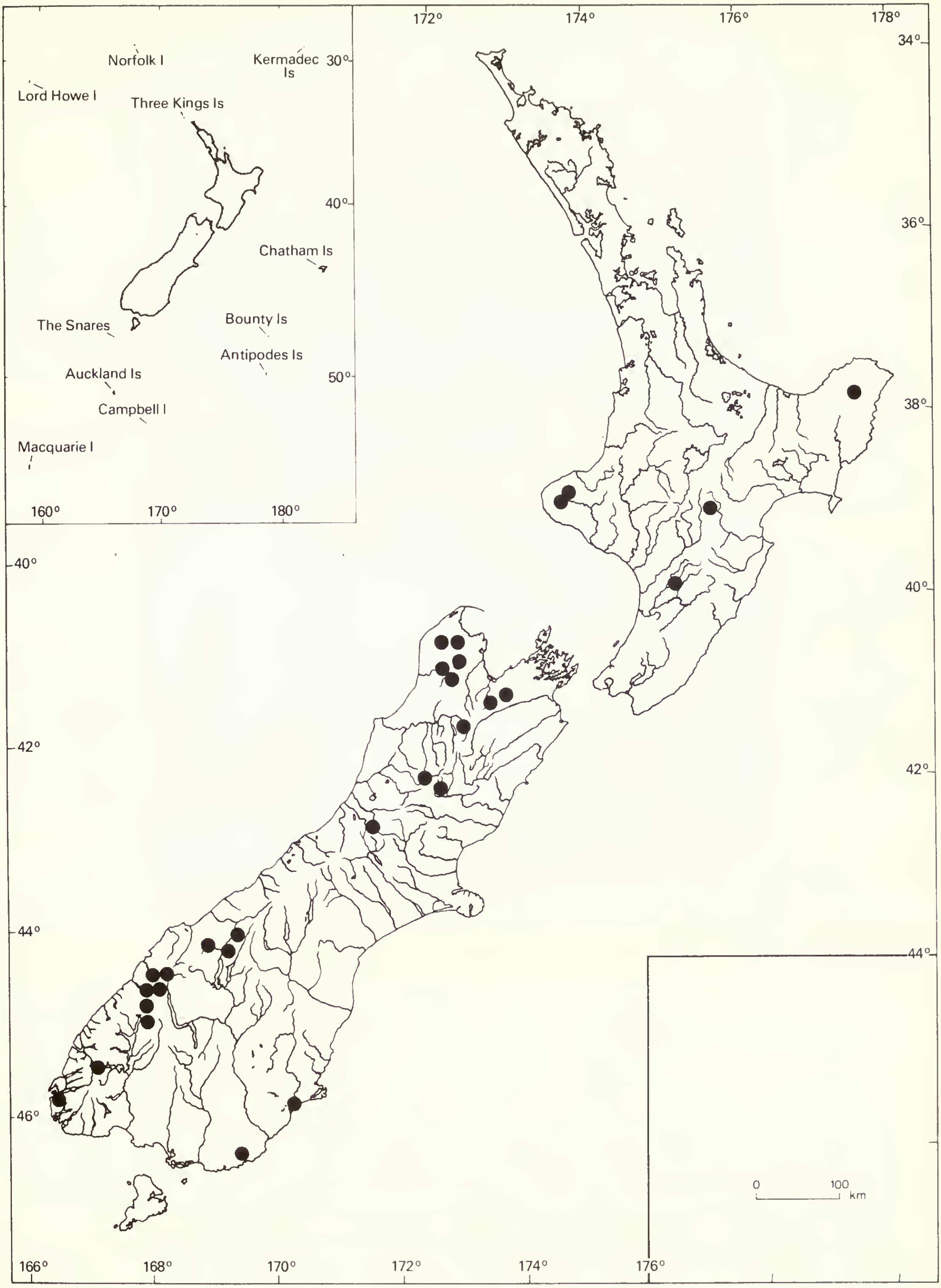

Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
40°
50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 65 Distribution of *Pseudocyphellaria fimbriata*.

phyllidia are generally margined with glistening, minute tomental hairs. The upper surface is coriaceous, minutely areolate-scabrid (× 10 lens), often suffused red-brown at apices. *P. fimbriata* has a white medulla, a green photobiont, and a pale red-brown to dark brown velvety tomentose lower surface, with numerous, prominent, white pseudocyphellae. Apothecia sessile to subpedicellate, the exciple well-developed, coarsely verrucose-areolate, ± patchily tomentose. Spores pale yellow-brown, broadly ellipsoid, 3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)]. Individuals are rather brittle and fragile when dry.

Variation: The species shows rather little variation in morphological characters throughout its range. It is distinguished from *P. coriacea* by the marginal and laminal phyllidia, and from *P. pubescens* which has entire – margined, ± uniformly tomentose lobes, yellow pseudocyphellae below, black apothecial discs which are normally grey-white pruinose, and a chemistry containing different hopanes, plus several depsides, pigments, and metabolites of the stictic acid complex. *P. fimbriata* differs also from *P. gretae*, a phyllidiate species having densely tomentose lobes and no detectable chemistry, and from the blue-green *P. fimbriatoides* which also has marginally pubescent phyllidia, but thinner, broader lobes which are glossy and much reminiscent of *Peltigera*.

Distribution: (Fig. 65) Rather rare and restricted in North I., from Mt Hikurangi (lat. 37°50′S), Mt Egmont, Kaimanawa Range, and the southern Ruahine Range. In South I., from the mountains of north-west Nelson to Fiordland, close to or west of the Main Divide, and on the east coast from Banks Peninsula to Invercargill, sea-level to 1500 m.

Habitat ecology: *Pseudocyphellaria fimbriata* is mainly a rain-forest species, constantly found in areas with a rainfall of 1600–6500 mm annually, and with spasmodic occurrence in drier areas (800–1600 mm annually). It is most commonly collected in *Nothofagus* forests close to and west of the Main Divide in South I., from areas having both high precipitation and a high number of rain days (100–250 days per annum). In the northern part of its range (Mt Hikurangi in the Raukumara Range), *P. fimbriata* occurs on exposed rocks with *Toninia bullata* in subalpine scrub, but elsewhere it grows on mossy stumps, mossy rocks, and most commonly on tree trunks in *Nothofagus* forest, or more rarely in the southern part of its range in lowland coastal forest.

Well-developed specimens form large, often irregular, rosettes on tree trunks in medium to well-lit habitats with sufficient moisture. Prominent colonies are seen near forest margins or in rather open forest, and the species is not found in low-light habitats. It is an epiphyte of the following phorophytes: *Dracophyllum traversii*, *Griselinia littoralis*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Phyllocladus alpinus*, and *Weinmannia racemosa*.

P. fimbriata associates mainly with other large species of *Pseudocyphellaria* including *P. colensoi*, *P. coriacea*, *P. degelii*, *P. gretae*, *P. homoeophylla*, *P. pickeringii*, and *P. pubescens*, and species of *Menegazzia*, *Psoroma*, *Sphaerophorus*, and *Usnea*.

Specimens examined: 60.

22. Pseudocyphellaria fimbriatoides D. Galloway & P. James **Fig. 66**

in *Lichenologist* **15**: 142 (1983). Type: New Zealand, South I., Canterbury, Banks Peninsula, below summit of Mt Sinclair, 670 m, on rocks on forest floor in dense bush, 14 February 1980, *J. A. Elix* (CHR 381117! – holotype).

Stictina fragillima var. *myrioloba* Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31**: 27 (1892). – *Sticta fragillima* var. *myrioloba* (Müll. Arg.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21**(3/13): 32 (1896). Type: New Zealand, sine loco, *C. Knight* 323 (G! – holotype).

Pseudocyphellaria hamataoides D. Galloway & P. James in *NZ Jl Bot.* **16**: 521 (1978), nom. nud. (Art. 32.1).

Morphology: *Thallus* 5–10(–15) cm diam., irregularly spreading, closely attached, corticolous, saxicolous, terricolous. *Lobes* variable, broad and elongate (1 × 5 cm) to short and rounded (2–8 mm diam.), apices discrete, contiguous or imbricate, complex-imbricate centrally, plane or ± canaliculate. *Margins* entire, sinuous, ascending, ± rounded or shallowly

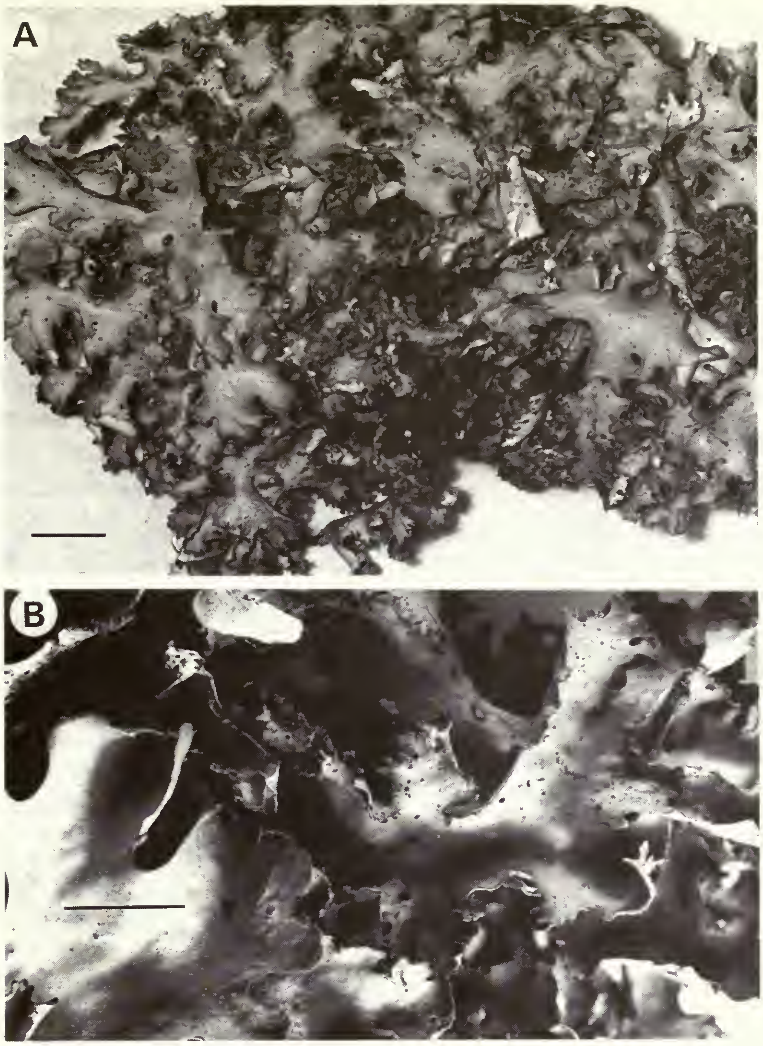


Fig. 66 *Pseudocyphellaria fimbriatoides*. Nelson, Rough Creek, Maruia Valley, *Galloway* (CHR 379945). A. Scale = 1 cm. B. Scale = 5 mm.

incised, sinuses semi-circular, crenate, ragged, lacerate, and ± densely phyllidiate, glabrous or minutely glistening-pubescent, slightly thickened below. *Upper surface* dark slate blue, suffused red-brown at apices when moist, pale greyish fawn, dark brownish or livid at apices and margins when dry, coriaceous, smooth or shallowly dimpled, glossy in parts or matt, often minutely granular white-papillate (× 10 lens), without soredia, isidia, maculae or pseudocyphellae. *Phyllidia* marginal, lobulate, dorsiventral, simple, bifurcate to ± coralloid-branched, constricted at base, scattered and ± solitary to densely crowded 0·1–2 mm tall, marginally pubescent-tomentose, glistening. *Medulla* white. *Photobiont Nostoc*. *Lower surface* white and ± glabrous, shining, smooth to minutely wrinkled or pitted at margins, ± tomentose, pale to dark brown or ± blackened centrally, tomentum thin, short, and velvety to woolly-arachnoid, entangled. *Pseudocyphellae* white, scattered, rather sparse to moderately common, 0·05–0·2 mm diam., slightly punctate-impressed, flat or very shallowly convex, sunk in tomentum at centre. *Apothecia* sessile, constricted at base, rather rare scattered, submarginal to laminal, 0·2–2·5 mm diam., shallowly concave at first, becoming plane and at length convex, disc pale orange-yellow to pale red-brown, matt, epruinose, smooth, margins pale, persistent, exciple pale whitish buff, translucent when moist, delicately arachnoid-scabrid, margins darker than disc when moist.

Anatomy: *Thallus* 120–185(–240) µm thick. *Upper cortex* 27–34 µm thick, outermost 7–11 µm pale straw-yellow, cells compressed, internally cells thin-walled, colourless, rather loosely arranged, 4·5–11·5 µm diam. *Photobiont layer* 45–57 µm thick, *photobiont Nostoc*, cells to 7 µm diam. *Medulla* 30–75(–120) µm thick, colourless, hyphae 4–5 µm diam. *Lower cortex* 25–32 µm thick, lowest 8–10 µm dark red-brown, the remainder colourless, cells thin-walled, similar to those of upper cortex. *Tomental hairs* 4–5 µm thick, colourless to pale yellow-brown, 30–80 µm long, single, rarely in fascicles. *Apothecia: Exciple* 90–185 µm thick, outermost 10 µm pale yellow-brown, the remainder colourless, cells densely conglutinate, thick-walled at margins, thinner and more loosely arranged internally, 11–15(–22) µm diam. *Hypothecium* 54–75(–90) µm thick, pale straw-yellow to dilute yellow-brown, changing blue-green on addition of K. *Thecium* colourless, 110–120 µm tall, without granules or oil droplets; *epithecium* 18–22 µm thick, dilute yellow-brown, unchanged in K. *Asci* 68–80 × 13·5–18 µm. *Ascospores* fusiform-ellipsoid, pale brown, 1-3-septate, straight or curved, 27–32 × 7–9 µm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria fimbriatoides* is an endemic species having rather variable, though ± broad lobes, with conspicuously phyllidiate margins (Fig. 70B), the phyllidia having marginal, glistening tomental hairs. The upper surface is coriaceous, ± glossy in parts (reminiscent of some species of *Peltigera*), and minutely granular, white papillate (× 10 lens). It has a white medulla, a blue-green photobiont, and a lower surface that is glabrous marginally, and pale to dark brown tomentose centrally with scattered, small, white pseudocyphellae. Apothecia are rare, sessile, the exciple pale whitish buff, delicately arachnoid-scabrid. Spores pale brown, 1-3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)].

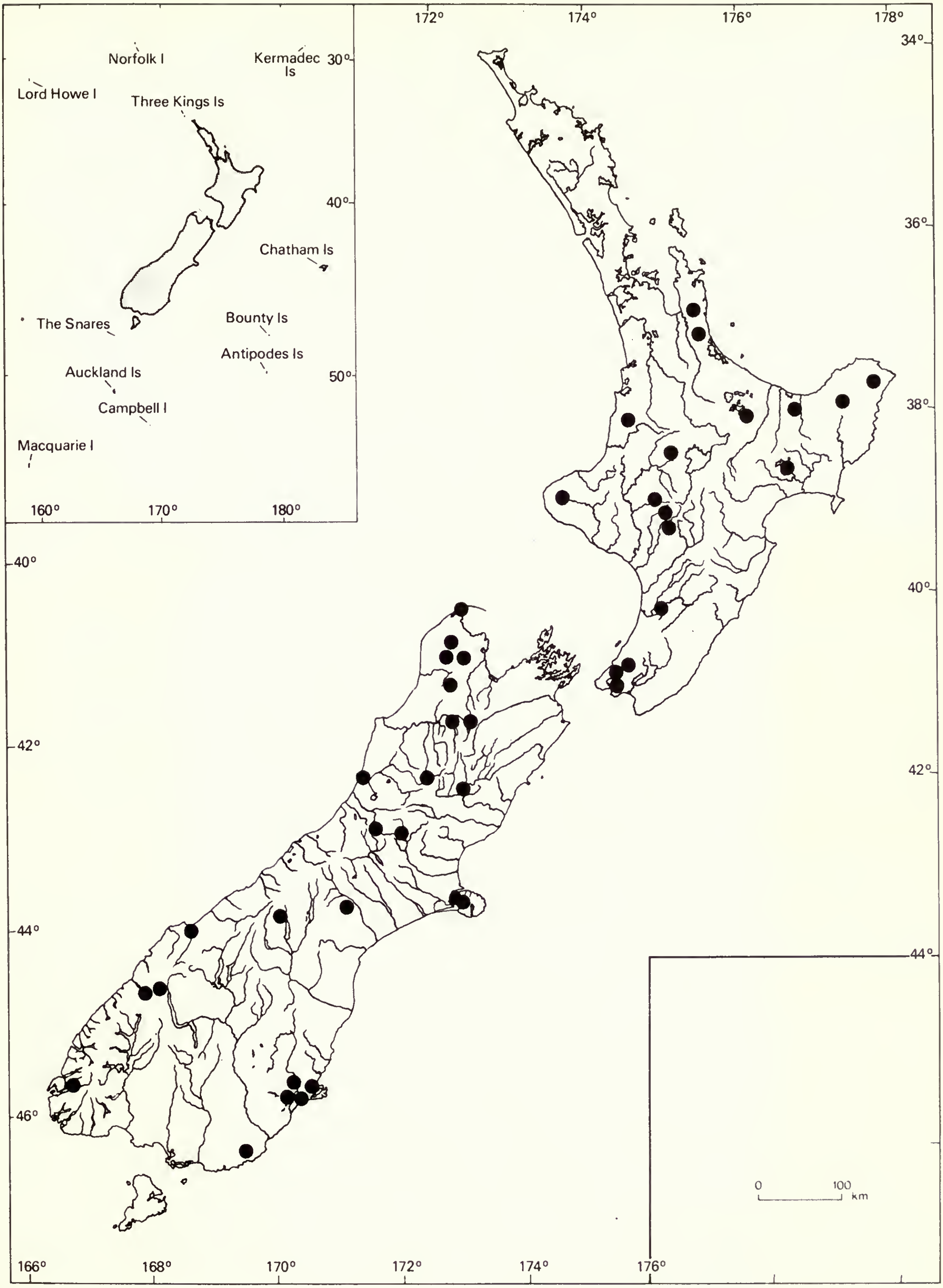
Variation: The lobes of *P. fimbriatoides* are rather variable in shape and in width and length, and also the phyllidia vary in numbers from sparse to densely crowded. This species is closely related to *P. dissimilis* and in many situations the two taxa are sympatric. They are distinguished by the tomentose phyllidia which are characteristic of *P. fimbriatoides*. Occasionally, *P. dissimilis* produces laminal and/or marginal phyllidia (normally it has terete, simple to branched isidia) but these are never marginally tomentose, and true isidia are never formed in *P. fimbriatoides*. *P. fimbriatoides* is also distinct from the australian species *P. insculpta* which has an identical chemistry and highly divided lobes which at times appear phyllidiate, but the margins of the lobes are never tomentose, and the upper surface is distinctly punctate-impressed. The spores of *P. insculpta* are also longer and broader than those of *P. fimbriatoides*. *P. fimbriatoides* is distinct from *P. fimbiata* which has a green photobiant, and thicker, more coriaceous lobes with a distinctive areolate-scabrid upper surface; it is not a photosymbiodeme of this species.

Distribution: (Fig. 67) North I., from Coromandel Peninsula (lat. 37°S) to Cook Strait, and in South I., from north-west Nelson to Southland, both east and west of the Main Divide, sea-level to 1200 m.

Habitat ecology: *Pseudocyphellaria fimbriatoides* along with *P. dissimilis* is, in the main, a shade-loving species and is most commonly collected from low-light, moist, cool habitats, on the forest floor (on both rocks and soil), at the base of tree trunks, and on tree roots deep in the forest interior, or along stream beds. It also grows on damp soil, on shaded rock faces, and can even withstand periodic inundation on stream bed boulders. It is known from the following phorophytes: *Cordyline australis*, *Beilschmiedia tawa*, *Melicytus ramiflorus*, *Metrosideros lucida*, *Nothofagus fusca*, *N. solandri* var. *cliffortioides*, *Podocarpus totara*, *Pseudopanax crassifolius*, *Pseudowintera colorata*, and *Senecio eleagnifolius*.

Other lichens growing in deeply shaded situations with *P. fimbriatoides* include *Lobaria retigera*, *Pseudocyphellaria cinnamomea*, *P. dissimilis*, and *Sticta caliginosa*.

Specimens examined: 67.


Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
50°
Auckland Is
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
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100
km

Fig. 67 Distribution of *Pseudocyphellaria fimbriatoides*.

23. **Pseudocyphellaria glabra** (J. D. Hook. & Taylor) Dodge **Figs 68, 69, 70**

in *B.A.N.Z.R.E. 1929–31 Repts* B, **7**: 79 (1948). – *Sticta glabra* J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 647 (1844). – *S. freycinetii* var. *glabra* (J. D. Hook. & Taylor) Zahlbr., *Cat. Lich. Univ.* **3**: 347 (1925). – *P. freycinetii* var. *glabra* (J. D. Hook. & Taylor) Räsänen in *Annln Bot. Soc. zool.-bot. fenn. Vanamo* **2** (1): 35 (1932). Type: Auckland Islands, *J. D. Hooker* (FH! – lectotype, fide Dodge (1948: 80); BM! – isotype) [see note 1].

Sticta delisea Delise in *Mém. Soc. linn. Normandie* **2**: 94 pl. 9, fig. 32 (1825) nom. superfl. (Art. 63.1). – *Pseudocyphellaria delisea* (Delise) D. Galloway & P. James in *Lichenologist* **12**: 297 (1980). – *S. freycinetii* var. *delisea* (Delise) Church Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 281 (1855). Type: 'Ile de King. Nouvelle Hollande, ex Herbar Commerson. Don de mon estimable ami A. L. A. Fée', ?*Leschenault de la Tour* (PC-LENORMAND! – lectotype; BM!, G!, L 2091–393!, PC-THURET!, VER! – isotypes) [see note 2].

Sticta freycinetii var. *isidioloma* Nyl. in *Bull. Soc. linn. Normandie II*, **2**: 504 (1868). Type: New Zealand, sine loco, *D'Urville* (H-NYL 33454! – holotype).

Parmelia isabellina Krempelh. in *Verhandl. zool.-bot. Ges. Wien* **30**: 338 (1881). Type: Australia, Mt Ellery, Gippsland, 1870, *Walter* (M! – holotype).

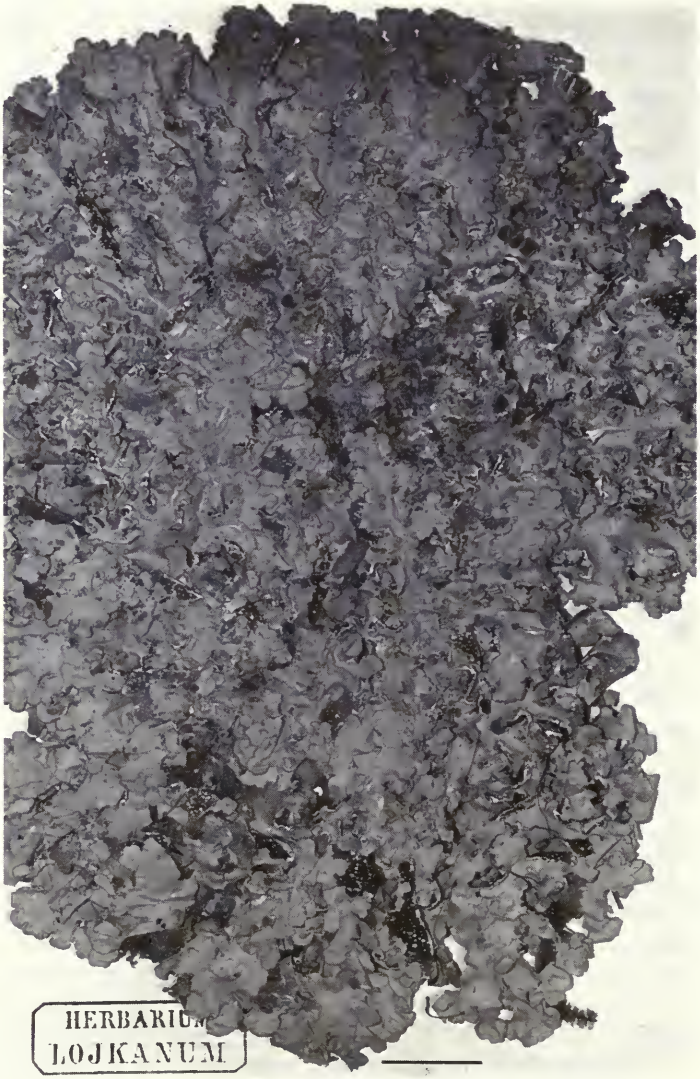


Fig. 68 *Pseudocyphellaria glabra*. New Zealand, *Helms* 77 (W). Scale = 2 cm.

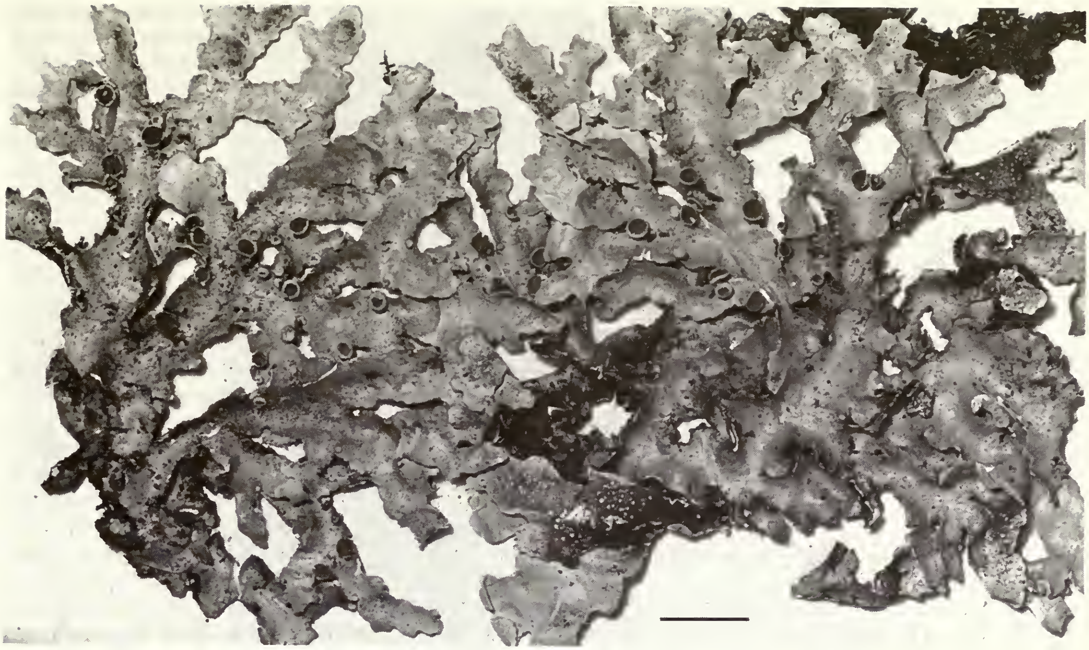


Fig. 69 *Pseudocyphellaria glabra*. Denniston, *Walker* (BM). Scale = 1 cm.

Sticta freycinetii var. *glabrescens* Müll. Arg. in *Flora, Jena* **66**: 23 (1883). – *Lobaria freycinetii* var. *glabrescens* (Müll. Arg.) Hellbom in *Bih. k. svenska Vetensk.-Akad. Handl.* **21**(3/13): 41 (1896). Type: New Zealand, Middle Island [South I.], *D. Lyall* (G 003023! – lectotype).

Sticta freycinetii var. *conjungens* Müll. Arg. in *Flora, Jena* **66**: 24 (1883). Type: Australia, Moe, Gippsland, *Webb* ex F. v. Mueller (G 002071! – holotype; MEL! – isotype).

Sticta freycinetii var. *prolifera* Müll. Arg. in Flora, *Jena* **66**: 24 (1883). Type: Australia, Moe, Gippsland, *Webb* ex F. v. Mueller (G 003054! – lectotype; MEL! – isotype).

Sticta freycinetii var. *tenuis* Müll. Arg. in *Flora, Jena* **66**: 24 (1883). Type: New Zealand, Kaipara, *S. Mossmann* ex herb. Babington, 1879 (G 002096! – lectotype).

Note 1: *Sticta glabra* J. D. Hook. & Taylor

Thomas Taylor's description of *Sticta glabra* (Hooker & Taylor, 1844: 647) gives an accurate account of the isidiate upper surface 'gemmis marginalibus minutis planis oblongis' and also records true apothecia for the first time 'apotheciis marginalibus subsessilibus concavis extus villosis disco fusco-olivaceo demum nigro margine lacero gemmifero'. The new species was recorded from 'Lord Auckland's group, Campbell's Island, Falkland Islands, Cape Horn and Van Diemen's Land' with the comment 'A span or more wide; unaltered by moisture, *apothecia* a little larger than turnip seed. Margins of the lobes raised and much waved. Falkland Island specimens have the lobes very wide'.

While helping Hooker with the initial publication of the lichens of the Antarctic voyage (1839–1843), Taylor wrote several times of his difficulties with the species of *Sticta* that Hooker had collected. 'The Stictae form a prominent feature of lichenological life in Antarctic regions. I am almost afraid that I have made too many new species. I know not how to help it. Montagne incidentally mentions 'Sticta Delisei' without any reference . . . , perhaps it is one of our new ones, I have no means of finding out what Montagne means' (Taylor Correspondence, Royal Botanic Gardens Kew, Director's Correspondence **103** (50), 31 October 1844). Further, after having submitted to Hooker the manuscript of *Lichenes Antarctici* [on 2 November 1844] in which nine new species of *Sticta* were described, Taylor observed 'I find it most difficult without seeing the coloured plates to compare the descriptions of Antarctic Lichens which you have kindly copied out with your collected species. And I have the most lively apprehensions lest some of the species I have believed to be new may turn out to be described already. It is for you my dear Sir, after receiving back your lichens to compare the new ones, especially the Stictae . . . I have not Delise's Monograph' (Taylor Correspondence . . . **103** (53), 15 November 1844).

Joseph Hooker visited Montagne in Paris in 1845 (Galloway, 1977*b*) and saw the extensive collections of French, Southern Hemisphere, and Antarctic lichens in the herbaria of Montagne and Webb and possibly

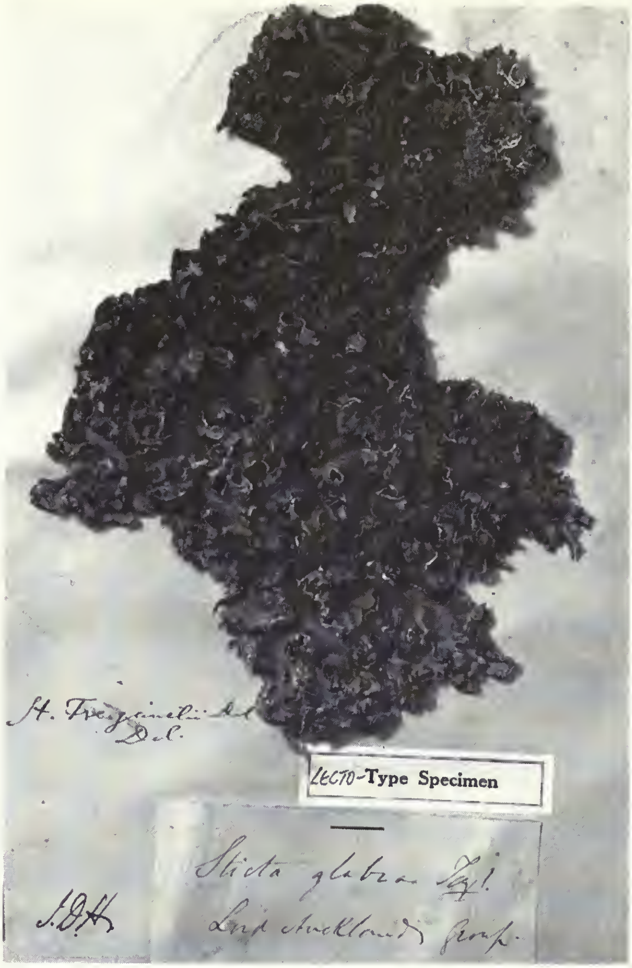


Fig. 70 *Sticta glabra*. Isotype (BM). Scale = 1 cm.

also material cited by Delise (1825*a*) in his monograph of *Sticta*. He undoubtedly saw *Sticta freycinetii* and realized the similarity of this South American species to the recently described *S. glabra*, for in the first part of *Flora Antarctica* he made *S. glabra* a synonym of *S. freycinetii* with the comment 'An exceedingly variable plant, of which we have added a character, that of Delise being imperfect [a recognition that the apothecia in the type of *S. delisea* were not true apothecia but a fungal parasite]. The most obvious specific distinction lies in the pubescent apothecia with fimbriated margins to the cups, to which may be added, the pale colour, and the wrinkled margins of the lobes, which are sometimes extremely concave. In alpine specimens the thallus is often quite smooth underneath, with the margins singularly crumpled. The colour varies, underneath it is of all shades, from black to a dirty yellow. Cape Horn and Falkland Island specimens are more plane, with the lobes and apothecia larger' (Taylor & Hooker, 1845: 198).

Examination of authentic material of *S. glabra* annotated by Taylor (BM, FH – 17 specimens seen from Auckland and Campbell Is, Tasmania, Hermite I., Falkland Is) shows that material from Hermite I. and the Falklands is *Pseudocyphellaria freycinetii* while the South Pacific material is *P. glabra*. Hooker (1847:528) realized that his earlier circumscription of *S. freycinetii* included two different taxa and provided a coloured plate (pl. CXCVI) of true *P. freycinetii* with the note 'We have added a figure of this much-disputed species, concerning which we have fallen into an error in the previous part of this work, having regarded it as synonymous with the *S. glabra* of Lord Auckland's group and Tasmania (probably the *S. delisea* Fée), and which differs from the *S. freycinetii* principally in the very shallow, not deeply cupped apothecia'. Babington (1855:281) in recording *S. freycinetii* var. *delisea* from New Zealand ignored the presence of isidia as a distinguishing character and declared 'A careful consideration of a large number of specimens has convinced me that the *Sticta freycinetii* of the two parts of the 'Flora Antarctica' are only forms of one and the same species'.

Du Rietz (1924), in emending *Pseudocyphellaria freycinetii* to include only non-isidiate taxa, included material referable to *P. glabra* in the synonymy of *P. chloroleuca* not having seen authentic material of *Sticta chloroleuca* which is an isidiate species quite distinct from *P. glabra.* Galloway & James (1980:297) followed Du Rietz in making *P. chloroleuca* a synonym of *P. glabra*, an error which is discussed further in Galloway (1986*b*), and in this paper (see above under *P. chloroleuca*, p. 85).

Dodge (1948) discusses the typification of *Sticta glabra* from material in Taylor's herbarium (FH) and chooses a fertile, Auckland I. specimen as lectotype (Dodge, 1948:80), a treatment which is adopted here in accordance with Art. 8.1 since it predates the lectotypification of *S. glabra* made by Galloway & James (1980: 297).

Note 2: *Sticta delisea* Delise

A. L. A. Fée described the monotypic genus *Delisea* for a curious Southern Hemisphere lichen differing from any species of *Sticta* then known, by the singular nature of the apothecia. It was collected from King Island in Bass Strait separating Australia and Tasmania. Fée (1824–1825: xcv, ci, tab. 2, fig. 15) named the species *pseudosticta* and illustrated it with a life-like coloured engraving. *Delisea* Fée, a later homonym of *Delisea* Lamouroux (Rhodophyta), was renamed *Plectocarpon* by Fée (1824–1825: 151). Later in the same year the material was sent to Delise who included it in his *Sticta* monograph as *S. delisea* (Delise 1825*a*), attributing the epithet to Fée. The material examined and described by Delise was recently discovered in PC-LENORMAND (Hawksworth & Galloway, 1984; Galloway & James, 1986) and is labelled in Delise's hand 'Ile de King. Nouvelle Hollande. Ex herbar. Commerson. Don de mon estimable ami A. L. A. Fée'. Philibert Commerson (1727–1773), naturalist with L. A. de Bougainville on *La Boudeuse* and *l'Étoile* during the circumnavigation of 1766–1769, never visited King Island and it is likely that the Australian material incorrectly ascribed by Fée and Delise to Commerson came from a later French expedition to Australia. Nelson (1974, 1975) has shown that several plant records mistakenly attributed to La Billardière [the first French botanist to collect in Australia, Filson, 1976; Kantvilas, 1983; Galloway, 1985*a*] are properly assigned to Leschenault de la Tour, botanist to the expedition commanded by Nicolas Baudin which visited King I., in December 1801. It seems probable that Leschenault was the collector of the material described by Fée, and Delise (Galloway & James, 1986).

The type material from Delise's herbarium (now in PC-LENORMAND) shows the specimen to be a sterile, isidiate species of *Pseudocyphellaria* attacked by a lichenicolous fungus causing apothecia-like galls to develop on the thallus. Hawksworth & Galloway (1984) typified the genus *Plectocarpon* on the lichenicolous fungus element and designated the host lichen element as lectotype of the name *Sticta delisea.* However, *Sticta delisea* is a superfluous name for *Delisea pseudosticta*, since this latter name [erroneously printed as *Delisea sticticoides* (Delise 1825:94)] is cited as a synonym by Delise (Art. 63.1). The use of the name *Pseudocyphellaria delisea* in several recent accounts is therefore erroneous (e.g. Galloway, 1985*b*, 1986*b*; Galloway & James, 1980, 1986; Galloway *et al.*, 1983; Hawksworth & Galloway, 1984). The earliest valid name for this Southern Hemisphere isidiate species is therefore *Sticta glabra.*

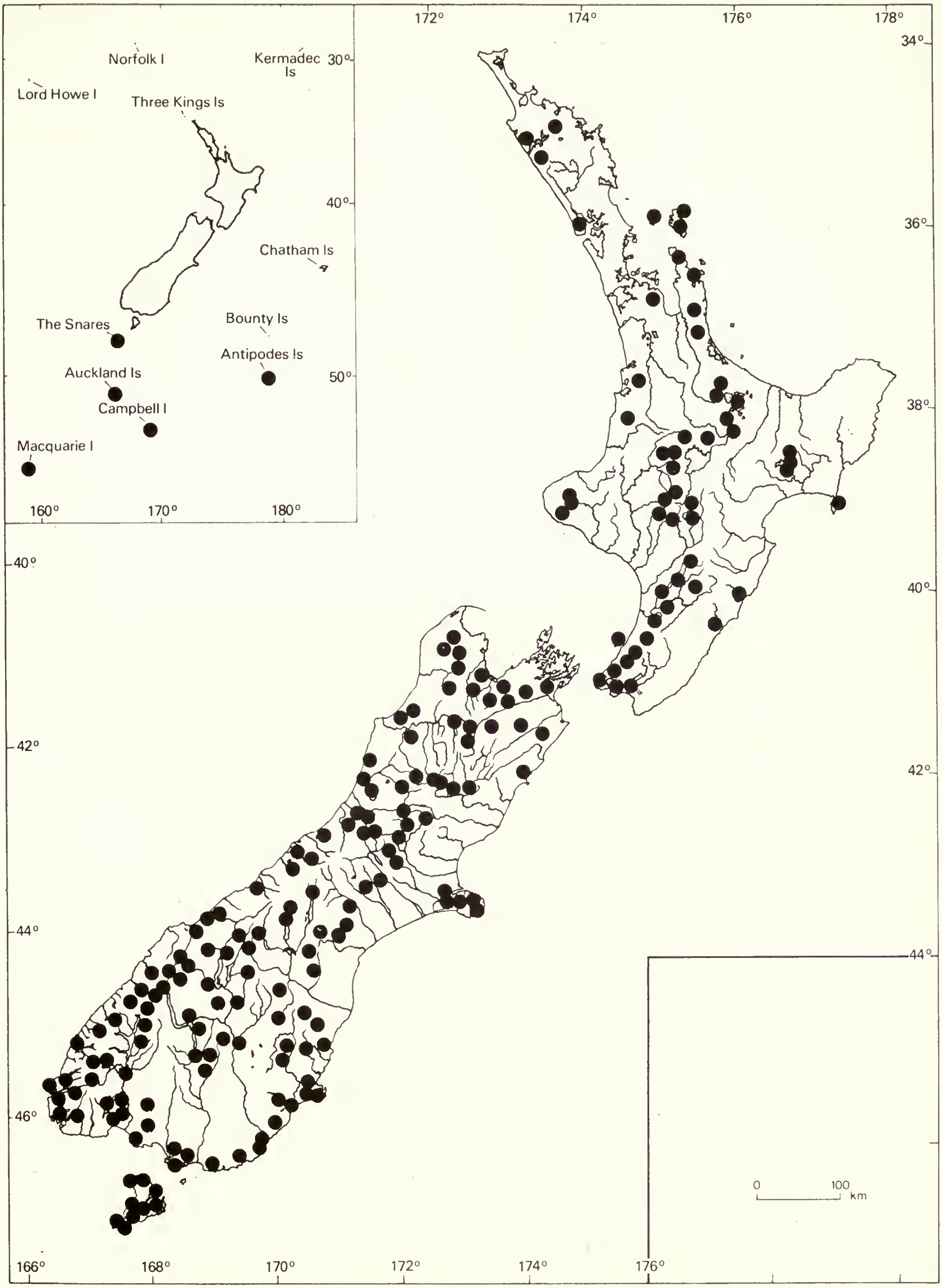
Morphology: Thallus rosette-forming to irregularly spreading, 5–10(–25 +) cm diam., loosely adnate centrally, margins closely attached to ± ascending, corticolous, terricolous, saxicolous. *Lobes* very variable, narrowly laciniate and almost straplike and discrete from margins to centre, 2–6 mm wide and 15–4 mm long, to 10–17 mm wide and ± imbricate-complex from near margins to centre. *Margins* entire, ± sinuous to crenulate or shallowly or deeply notched or incised becoming isidiate with age to somewhat erose-glomerulate. *Upper Surface* fresh lettuce green to pale greenish yellow when moist, pale greenish to yellowish fawn often suffused brownish at margins when dry (alpine forms ± whitish to ± red-brown or blackened in exposed sites), undulate, shallowly wrinkled or obscurely ridged in parts, never faveolate, alpine forms very coriaceous often conspicuously wrinkled and deeply cracked, cracking occasional to extensive, random, not in any pattern, matt to ± glossy, occasionally with small dimples, without soredia, maculae, phyllidia or pseudocyphellae. *Isidia* sparse to copiously developed, mainly marginal or from surface cracks, terete, fingerlike, mainly simple, occasionally furcate, 0·5–1 mm tall, often crowded-congested. *Medulla* white. *Photobiont* green. *Lower surface* smooth to irregularly wrinkled-shining, very variable, glabrous, pale buff or whitish to brown or brown-black in a narrow to wide marginal zone, tomentose centrally, or completely glabrous, or ± entirely tomentose from margins to centre, tomentum thin to thick and woolly, even, not tufted, pale brown to black, occasionally completely glabrous and black. *Pseudocyphellae* common, prominent, white, round to irregular, 0·1–1 mm diam., raised, verruciform-papillate, margins of papillae free from tomentum, decorticate area flat or shallowly excavate. *Pycnidia* occasional to rare, mainly marginal or submarginal, punctate-impressed, rather inconspicuous, 0·1 mm diam. or less, central ostiole pale red-brown, minute, surrounded by a slightly raised margin concolorous with thallus, often eroding and leaving small pits. *Apothecia* sessile to subpedicellate, sparse to occasionally crowded and deformed through mutual pressure, often absent, deeply to shallowly concave, plane to shallowly undulate and subconvex with age, round to irregular, 0·5–7 mm diam., margins entire to crenate-striate or occasionally ± stellate-ragged, formed from coarsely splitting edges of exciple, disc pale to dark red-brown, obscured at first by exciple, matt, epruinose, exciple translucent when moist, whitish to buff-pink when dry, brownish on storage in herbarium, ± arachnoid-tomentose at first and obscuring disc with a thick plug of tomentum, coarsely scabrid-areolate with age.

Anatomy: *Thallus* 135–200(–370) μm thick. *Upper cortex* 45–56 μm thick, upper 11–12 μm straw yellow, of necrotic or compressed cells appearing fibrous and ± periclinal, lower 30–40 μm colourless, thin-walled, 5–13 μm diam. *Photobiont layer* 35–45 μm thick, *photobiont* green, cells round, 9 μm diam. *Medulla* 90–250 μm thick, hyphae ± periclinally arranged, compact towards lower cortex, more loosely arranged near photobiont layer. *Lower cortex* 22–27 μm thick, outermost 11–12 μm dark red-brown (dissolving in K), inner zone straw-yellow to ± hyaline, cells thick-walled, 5–7 μm diam. *Tomental hairs* strongly septate, locules short, 4·5–7 μm long, slightly constricted at septa, red-brown, solitary or in fascicles, rather short, 35–110 μm long. *Apothecia: Exciple* 45–90 μm thick at margins, to 180 μm below disc, cells 7–11(–15) μm diam., colourless, in rows splitting away as pyramidal clumps or as thick-walled, short tomental hairs. *Hypothecium* 45–75 μm thick, dilute orange brownish or pale straw yellow. *Thecium* 65–80 μm tall, colourless; *epithecium* 11–13 μm thick, dilute yellow-brown to red-brown, dissolving in K, ± granular, colour external to tips of paraphyses. *Asci* 65–81 × 11–15μm. *Ascospores* pale yellow-brown, fusiform, apices pointed, mainly 1-septate, 3-septate at maturity, not thickened, (13·5–)15·5–20·5(–22·5) × 4·5–7 μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol, norstictic, stictic, cryptostictic, constictic, hypostictic (tr.), hyposalazinic (tr.), and usnic acids.

Distinguishing features: *Pseudocyphellaria glabra* is a widespread austral lichen having narrowly laciniate to broad, imbricate-complex lobes with entire, sinuous to crenulate or incised margins, often ± isidiate. Upper surface glossy, undulate, shallowly wrinkled, never faveolate, isidiate. Isidia marginal or laminal, often from surface cracks, terete, finger-like, mainly simple to occasionally furcate or ± palmate-flattened. It has a white medulla, a green photobiont, and a pale to dark brown or black, glabrous to tomentose lower surface with prominent white pseudocyphellae. Apothecia occasional, sessile to subpedicellate, exciple whitish to buff-pink, prominent, coarsely scabrid-areolate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)] with the addition of the stictic acid group of metabolites and usnic acid (±), which confers a yellow-green colour to the upper surface, especially in habitats exposed to full sunlight.

Variation: *Pseudocyphellaria glabra* is a very polymorphic species colonizing a wide variety of habitats in New Zealand from coastal forest and/or scrub, to *Nothofagus* forest, and mixed hardwood-*Nothofagus* forest, subalpine scrub at and above tree-line, and subalpine to alpine grasslands and herbfield. It shows a wide range of thallus morphology throughout these different habitats, lobes varying from narrow, discrete, and ± straplike, to broad, rounded, ± imbricate, and with a lower surface that may be entirely glabrous to centrally or entirely tomentose, pale buff or brown to entirely black. Thallus thickness varies a good deal depending on the degree of exposure to sun, frost, and wind. Shaded specimens from forest and scrub communities are pale green, ± deficient in usnic acid, and rather thinner and less coriaceous than exposed subalpine forms which tend also to be less isidiate, are more yellow, and often partially or totally blackened, or suffused red-brown. Some alpine forms are ± whitish or greyish and are generally very thick and coriaceous. All forms have characteristic terete (usually simple), finger-like isidia; these are often abraded, and tend to lie scattered on the upper surface. Forest forms are usually


Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
50°
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
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42°
44°
46°
0 100 km
166°
168°
170°
172°
174°
176°

Fig. 71 Distribution of *Pseudocyphellaria glabra*.

more richly isidiate (especially at the margins) than those from above tree-line. Although a wide diversity of thallus form exists in this species, there is no chemical variation observed.

Pseudocyphellaria glabra is the isidiate counterpart of the New Zealand endemic *P. homoeophylla*. It is also closely related to *P. corbettii*, a species having marginal phyllidia and broad lobes. The South American *P. freycinetii* is related to *P. glabra* and has a similar chemistry, but it lacks isidia and has larger, thinner, more folded, and papery lobes.

Distribution: (Fig. 71) Widely distributed from North Auckland (lat. 35°S) southwards to Stewart I., and the subantarctic islands (Snares, Auckland, Campbell, Antipodes, and Macquarie), coastal to alpine, sea-level to 2000 m.

Habitat ecology: *Pseudocyphellaria glabra* has the widest range and ecological tolerance of any species of *Pseudocyphellaria* in New Zealand, being known from all forest types, coastal and subalpine scrub, subalpine to high-alpine grassland and herbfield. It grows luxuriantly in the wettest areas of the country, in forests west of the Main Divide and especially in Fiordland, and is also found in the very driest areas, in Central Otago and eastern parts of South I. In forest and/or scrub associations it is an epiphyte of branches and trunks, and in some drier areas will grow on soil, on rocks, and amongst bryophytes. It has been collected from the following phorophytes: *Agathis australis*, *Aristotelia serrata*, *Coprosma foetidissima*, *Dacrycarpus dacrydioides*, *Dacrydium bidwillii*, *D. cupressinum*, *Dracophyllum latifolia*, *D. longifolium*, *Fuchsia excorticata*, *Griselinia littoralis*, *Hebe spp.*, *Kunzea ericoides*, *Leptospermum scoparium*, *Libocedrus bidwillii*, *Melicytus ramiflorus*, *Metrosideros lucida*, *M. umbellata*, *Myrsine australis*, *M. divaricata*, *Myrtus bullata*, *Nothofagus menziesii*, *M. solandri* var. *cliffortioides*, *Olearia colensoi*, *Pimelea* spp., *Pittosporum eugenioides*, *P. tenuifolium*, *Podocarpus hallii*, *P. nivalis*, *P. totara*, *Phyllocladus alpinus*, *Prumnopitys ferruginea*, *Pseudopanax edgerleyi*, *P. simplex*, *Pseudowintera colorata*, *Quintinia acutifolia*, *Rhopalostylis sapida*, *Senecio eleagnifolius*, *S. reinoldii*, and *Weinmannia racemosa*.

Pseudocyphellaria glabra is also found in subalpine bogs, straggling amongst tussocks, or on rock outcrops in subalpine grassland, and in herbfield at the lower limit of the high-alpine zone.

Specimens examined: 507.

24. **Pseudocyphellaria granulata** (Church. Bab.) Malme **Fig. 72**

in *Bih. K. svenska Vetensk.-Akad. Handl.* **25** (3/6): 21 (1899). – *Sticta granulata* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 281 (1855). – *S. richardi* var. *granulata* (Church. Bab.) Nyl. in *Mém. Soc. Imp. Sci. nat. Cherbourg* **5**: 335 (1857). – *Stictina carpoloma* subsp. *granulata* (Church. Bab.) Nyl., *Syn. meth. lich.* **1** (2): 338 (1860). – *Sticta carpoloma* var. *granulata* (Church. Bab.) J. D. Hook., *Handb. N. Zeal. fl.* **2**: 568 (1867). – *Phaeosticta granulata* (Church. Bab.) Tevisan, *Lichenotheca veneta* exs. 75 (1869). – *Lobaria granulata* (Church. Bab.) Kuntze, *Revis. gen. pl.* **3**: 384 (1893). Type: New Zealand, Middle Island [South I.], *D. Lyall* (BM! – holotype).

Babington (1855:281) says of *Sticta granulata*, 'Our Lichen resembles *S. pulmonacea* a good deal in its ample size and general mode of division, but seems to be as nearly allied to the preceding as to any other. The olive-green colour, the scrobiculated thallus, and, above all, the tendency of the plant to produce copious dirty coralline pulvinate soredia, often covering the centre, and the irregular, ill-developed, dirty yellow cyphellæ, are its most obvious characters. Found also in Tasmania by Gunn and by Hooker . . . The imperfectly-formed cyphellæ show a transition to the structure of the simple naked spots of *S. scrobiculata* and its allies, which constitute a section (*Lobaria*) not yet found in New Zealand'.

Robert Gunn's Tasmanian specimen, originally in Taylor's herbarium is labelled 'Sticta granulata Tayl. MSS' in Thomas Taylor's hand. In Taylor's herbarium (FH) four Gunn specimens so named by Taylor are preserved, together with one from Swan River [Western Australia] collected by James Drummond which is also named *S. granulata* Tayl., but which is referable to *Pseudocyphellaria neglecta*. In Babington's herbarium (BM), the holotype specimen is labelled by Babington 'S. granulata Tayl ! Bab. in Hook. Fl. N.Z.', so he obviously used Taylor's name. No New Zealand material of *P. granulata* is preserved in Taylor's (FH) herbarium.

Morphology: *Thallus* orbicular to irregularly spreading, 5–12(–25) cm diam., corticolous or saxicolous, loosely to closely attached centrally, margins ± free. *Lobes* deeply incised, ±

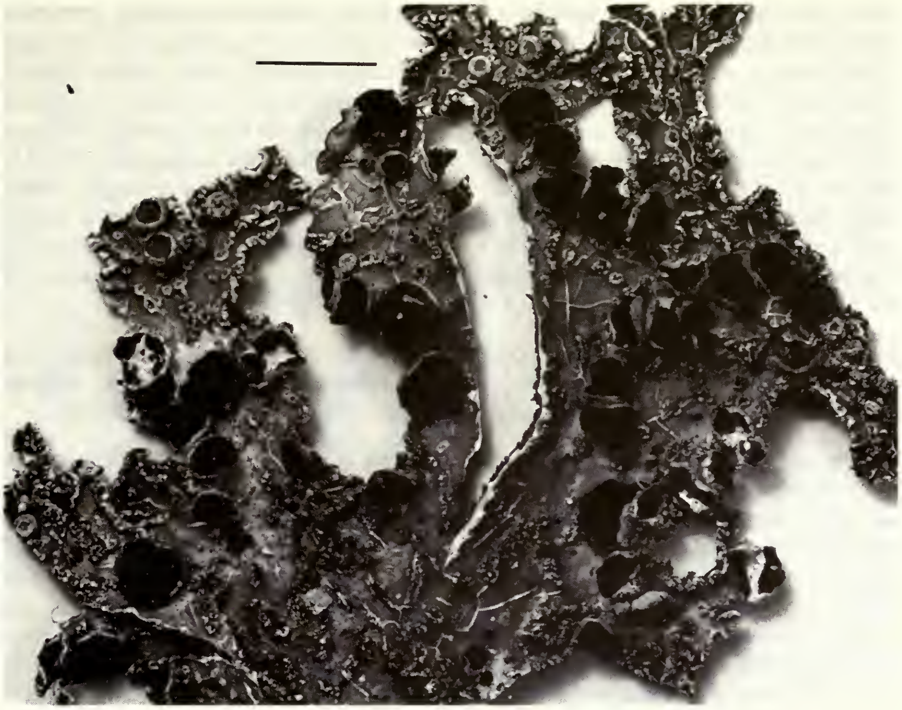

Fig. 72 *Pseudocyphellaria granulata*. Lake Te Anau, *Hale* 65085 (US). Scale = 5 mm.

linear-elongate to broadly rounded, 0·5–2·5 cm diam. and 1–5 cm long, discrete or contiguous at margins, ± complex-imbricate centrally. *Margins* very irregular, rarely entire, more often ragged, notched, incised, crenulate-lacerate, flat to sinuous and ± ascending, ± coarsely and densely sorediate, often eroded-white. *Upper surface* glaucous-green to olivaceous, often suffused greyish or blackened when moist, grey-fawn or glaucous yellowish, often ± blackened in exposed sites when dry, plane to sub-convex, undulate, dimpled, punctate-impressed, wrinkled-plicate to ± faveolate-reticulate, with erumpent, pustular soralia, often coalescing into lines or patches, often cracked or fissured, coriaceous, matt, without isidia, maculae, phyllidia or pseudocyphellae. *Soredia* eroding lobe margins and erupting in ± rounded, pustular soralia on lamina, also developing from breaks or fissures, coarse, granular-glomerulate, in dense clusters, pale olive greenish eroding whitish, often ± blackened, sometimes appearing pseudoisidiate. *Medulla* white. *Photobiont* green. *Lower surface* pale buff or whitish at lobe margins, black centrally, tomentose from margins to centre, or with a narrow, glabrous, pale buff, delicately wrinkled, shining marginal zone, tomentum thick, woolly. *Pseudocyphellae* frequent, conspicuous, white, round to irregular 0·1–1·5 mm diam., in shallow to well-developed papillae, margins black, slightly raised, prominent, often fissured, decorticate area flat, coarsely granular, sunk in tomentum. *Pycnidia* occasional, hemispherical, laminal, 0·2–0·5 mm diam., ostiole punctate, black, minute. *Apothecia* sessile to subpedicellate, rather rare, marginal and laminal, often most common towards lobe apices, 1·3 mm diam., round to irregular, contorted through mutual pressure, margins pale to dark red-brown, crenulate-roughened to ± tomentose, massive at first and completely obscuring disc in young fruits, disc black, matt or granular, coarsely white-pruinose at first, pruina uneven, ± areolate (× 10 lens), lost with age, exciple pale buff to red-brown, ± translucent when moist, roughened, granular-verrucose.

Anatomy: *Thallus* 165–280(360) μm thick, to 540 μm thick at cephalodia. *Upper cortex* 27–34 μm thick, upper 10–12 μm pale yellow-brown becoming faint violet in K, lower zone colourless, cells 6·5–13·5 µm diam. *Photobiont layer* 34–56 µm thick, *photobiont* green, cells rounded, to 11·5 µm diam. *Medulla* 90–200 µm thick, colourless, hyphae to 5 µm diam. *Lower cortex* 27–35 µm thick, red-brown, dark blue-green in K, densely conglutinate, cells 5–9 µm diam. *Tomental hairs* to 5 µm diam., in dense fascicles, red-brown, to 230 µm long. *Apothecia:Exciple* colourless, 120–200 µm thick, yellow-brown towards margins, cells 7–14 µm diam. *Hypothecium* 82–95 µm thick, pale yellow-brown to straw-yellow, unchanged in K. *Thecium* colourless, 100–110 µm tall, ± granular or with numerous oil droplets; *epithecium* 7–14 µm thick, smoky olive-grey to olive-brown, purple-violet in K. *Asci* 76–80 × 13–15 µm. *Ascospores* smoky grey to olive-brown, oval-ellipsoid, thickened 1-septate to 3-septate, apices pointed, sometimes papillate, septum variable in thickened 1-septate spores 1·5–4·5 µm thick, locules uneven, irregular-deformed, 22·5–32 × 9–11·5 µm.

Chemistry: Hopane-7β, 22-diol (tr.), hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α, acetoxyhopane-7β, 22-diol (tr.), methyl virensate, physciosporin, norstictic (tr.), stictic, cryptostictic (tr.), and constictic acids [Code B of Wilkins & James (1979)].

Distinguishing features: *Pseudocyphellaria granulata* is an austral species having deeply incised, linear-elongate to broadly rounded lobes, with irregular, ragged or incised-crenulate, sorediate-eroded margins. The upper surface is plane to punctate-impressed to ± faveolate in parts, with erumpent, pustular soralia at margins, and scattered over, to thickly covering the upper surface, or ± restricted to reticulate ridges. The medulla is white, the photobiont green, and the lower surface ± uniformly black, or with a pale buff to whitish glabrous marginal zone, thickly tomentose and with conspicuous, white pseudocyphellae. Apothecia are sessile to subpedicellate, rather rare, the disc black, coarsely white-pruinose at first, the exciple pale buff to red-brown, roughened-granular-verrucose. The epithecium is smoky grey to olive-brown, becoming purple-violet in K. Spores are grey to olive-brown, thickened 1-septate to 3-septate. The chemistry is distinctive, containing physciosporin as a major metabolite [Code B of Wilkins & James (1979)].

Variation: *Pseudocyphellaria granulata* is a rather variable species, showing a wide diversity of lobe shape and size, and with a surface texture varying from plane to reticulate-faveolate, depending on local microclimate and microhabitat conditions. The numbers and position of soralia also show a wide amplitude of variation from ± marginally sorediate forms to forms ± totally sorediate in a dense laminal crust. Soredia are always present and are the major taxonomic character differentiating this species from all other related white-medulla species. The non-sorediate species *P. faveolata* has an identical chemistry and in many habitats is sympatric with *P. granulata.* The two species constitute a species pair, and occur widely together throughout the austral zone. In some recent accounts, records of *P. granulata* from northern, offshore islands (Hayward & Hayward, 1978, 1980, 1982*a*, 1982*b*, 1984) refer to *P. haywardiorum.*

Distribution: (Fig. 73) North I., south of lat. 36°50′S, to Cook Strait, and in South I., from Nelson to Fiordland, also in Stewart I., lowland to subalpine, sea-level to 1000 m.

Habitat ecology: *Pseudocyphellaria granulata* is a common epiphyte of lowland coastal forest and scrub, and especially of successional vegetation (notably *Fuchsia* and *Leptospermum*) in altered sites, though it is also often found near treeline and in subalpine scrub. It is a moderately photophilous species and will not tolerate deep shade, and most commonly associates with other species of *Pseudocyphellaria* in areas of moderate to high rainfall. It will also colonize rocks in tussock grassland and grows on dead stumps as well as the following phorophytes: *Coprosma* spp., *Cordyline australis*, *Dacrycarpus dacrydioides*, *Dracophyllum subulatum*, *Fuchsia excorticata*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *Myrsine australis*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Picea abies*, and *Weinmannia racemosa.*

Specimens examined: 65.

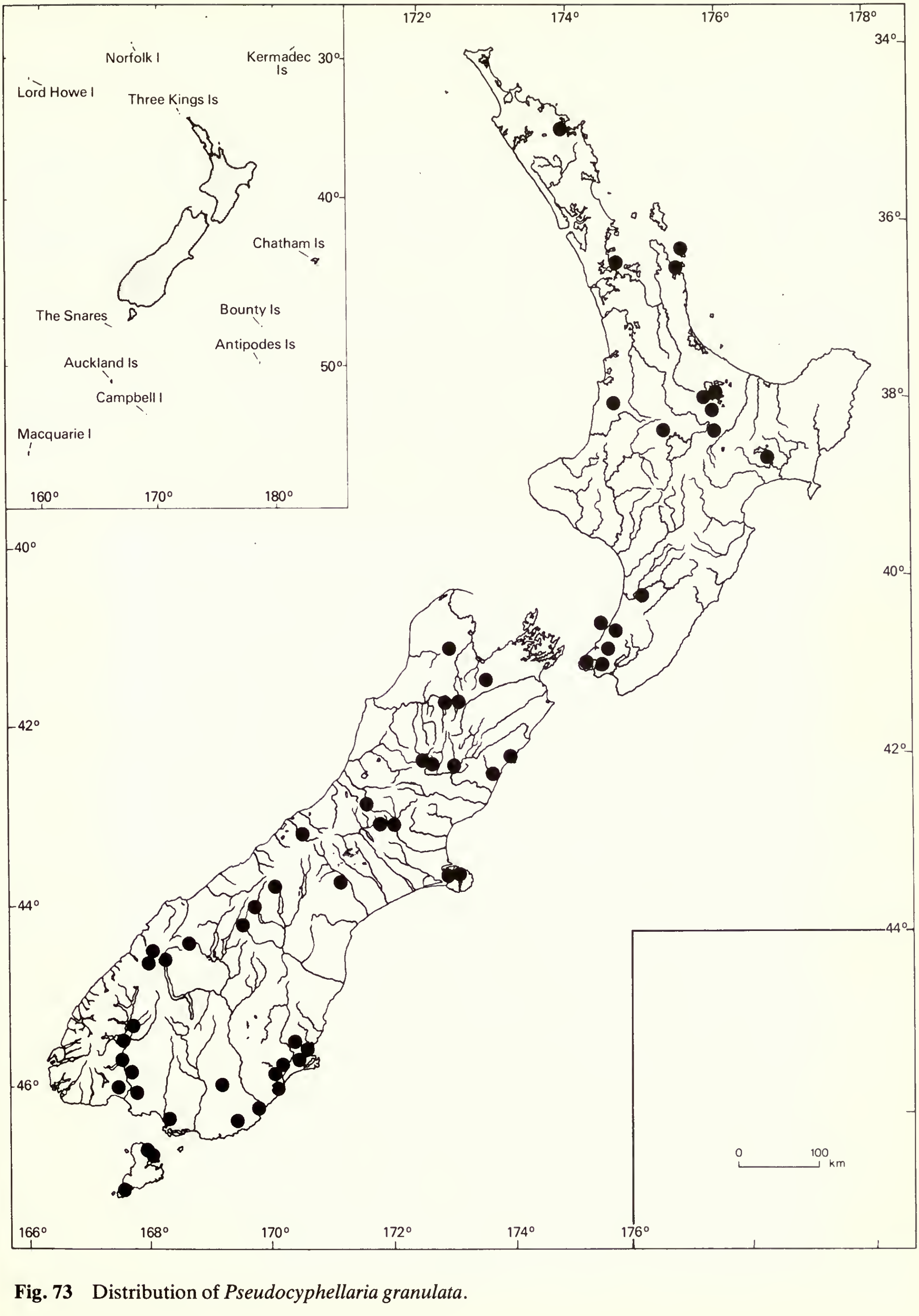
Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
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Fig. 73 Distribution of *Pseudocyphellaria granulata*.

25. Pseudocyphellaria gretae D. Galloway **Fig. 74**

in *Lichenologist* **15**: 143 (1983). Type: New Zealand, South I., Cantebury, Boyle River near Lewis Pass, on bark of *Nothofagus menziesii*, 13 September 1981, *D. J. Galloway* (CHR 381118! – holotype, BM! – isotype).

Pseudocyphellaria hirsutula D. Galloway & P. James in *NZ Jl Bot.* **16**: 521 (1978), nom. nud. (Art. 32.1)

Morphology: Thallus ± orbicular or spreading in irregular rosettes, 5–10(–18) cm diam., rather loosely attached from margins to centre, corticolous. *Lobes* sublinear-laciniate to broadly rounded, apices ± discrete to subimbricate, usually densely isidiate centrally, 0·5–1·5(–2·5) cm wide and 1–2(–5) cm long. *Margins* entire, delicately notched or incised to ± crenulate, often densely isidiate, slightly thickened below, markedly revolute at lobe apices. *Upper surface* bright lettuce-green, occasionally suffused brownish at margins when fresh, pale grey-green to glaucous-buff, yellowish olive or pinkish in parts when dry, becoming dark red-buff to brownish on storage, undulate, mainly convex, rarely plane to subconcave, shallowly and irregularly wrinkled or dimpled, never faveolate, internal cephalodia visible as small, rounded papillae 0·2–0·5 mm diam., texture rather delicate, densely to sparsely tomentose, tomentum white, silky, often abraded or absent in older parts, cortex below tomentum smooth to minutely scabrid-verrucose and reticulate-cracked, soredia, maculae, phyllidia, and pseudocyphellae absent. *Isidia* marginal and laminal, delicate, fragile, brittle, granular to coralloid, 0·2–0·5 mm tall, ± flattened, appearing squamiform, in rows or dense clusters, often spreading over surface

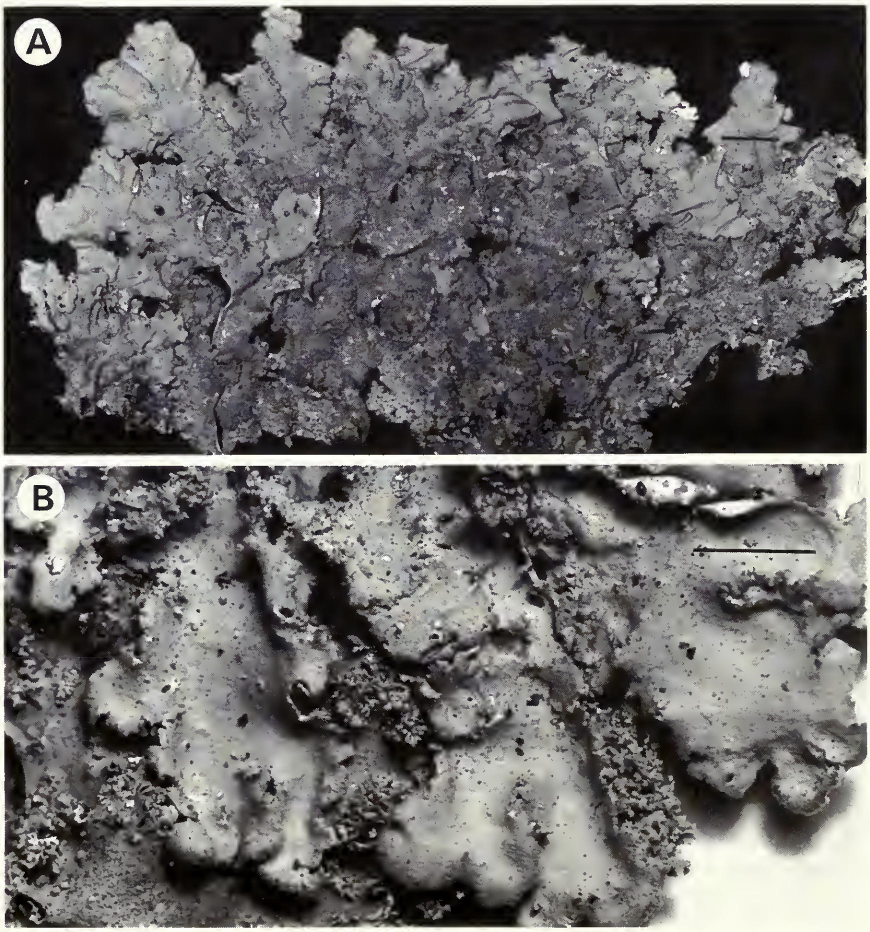


Fig. 74 *Pseudocyphellaria gretae*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 5 mm.

as a thick coralloid crust, ± uniformly tomentose. *Medulla* white. *Photobiont* green. *Lower surface* white, pale buff to pinkish or brownish centrally, densely tomentose from margins to centre, or with ± extensive glabrous patches centrally in older specimens, shallowly wrinkled or dimpled in parts, tomentum thick, silky, white, rather short. *Pseudocyphellae* minute, often inapparent, scattered, sparse to moderately common, ± obscured by tomentum, flat or slightly papillate, 0·05–0·3(–0·8) mm diam., round to irregular, mainly white, occasionally pale yellowish. *Pycnidia* rather rare, laminal, punctate to ± papillate, 0·1 mm diam. or less, ostiole red-brown. *Apothecia* very rare, marginal and laminal, sessile at first, becoming distinctly pedicellate, 0·5–2(–3·5) mm diam., shallowly to deeply concave, margins ± involute, ± isidiate-ragged often obscuring disc, disc dark red-brown to brown-black, matt, epruinose, exciple delicately scabrid-verrucose, tomentose, concolorous with thallus.

Anatomy: *Thallus* 105–202 µm thick. *Upper cortex* 34–45(–50) µm thick, upper surface very uneven splitting into irregular pyramidal areas (scabrosity), colourless to pale straw-yellow, cells 4·5–11·5 µm diam. *Tomental hairs* 45–140(–230) µm long, 7–11 µm thick, sparsely septate. *Photobiont layer* 23–27(–36) µm thick, densely compacted, *photobiont* green, 7–9 µm diam., *Dictyochloropsis*. *Medulla* 55–92(–120) µm thick, colourless, compact, hyphae 2·5–3·5 µm diam. *Lower cortex* 27–34(–45) µm thick, colourless or pale straw-yellow, cells 7–14 µm diam. *Tomental hairs* to 5µm diam., 45–135(–180) µm long, colourless. *Apothecia: Exciple* colourless, 90–140 µm thick, cells thick-walled, 9–15 µm diam. *Hypothecium* 45–73 µm thick, upper 20 µm colourless, remainder dilute orange-brown, unchanged in K. *Thecium* colourless, 100–120 µm tall; *epithecium* 7–21 µm thick, yellow-brown to red-brown, colour in gel external to tips of paraphyses, dissolving in K; *paraphyses* distinctly vacuolate (? oil droplets), moniliform at apices. *Asci* 78–90 × 11·5–15·5 µm. *Ascospores* brown, broadly ellipsoid, thickened 1-septate to 3-septate, locules lozenge-shaped, irregular, apices rounded or pointed 23–29·5 × 11·5–13·5 µm.

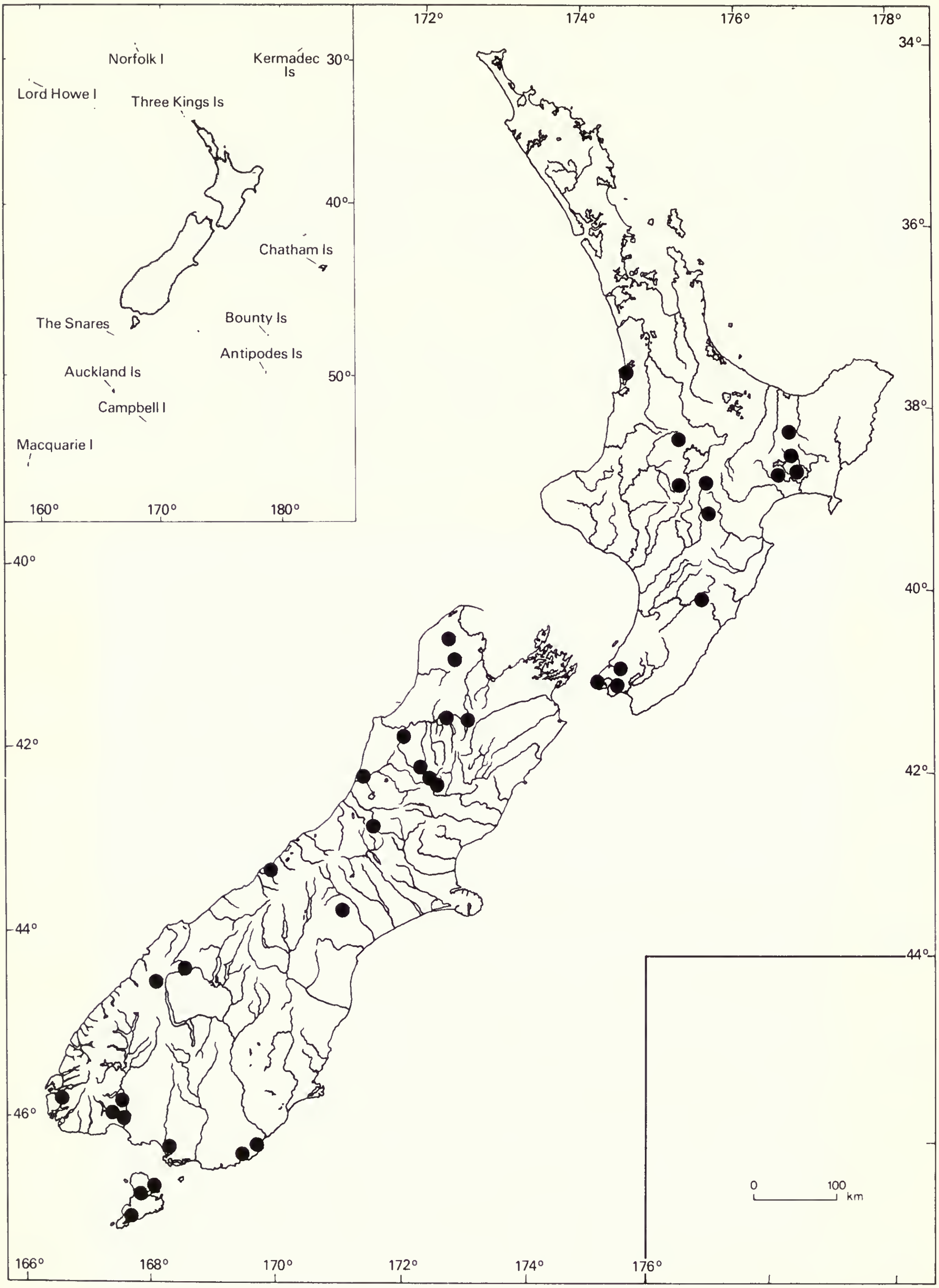
Chemistry: t.l.c. negative.

Pseudocyphellaria gretae is named for the late Greta Du Rietz who collected lichens widely throughout New Zealand in 1926–1927 with her husband G. Einar Du Rietz.

Distinguishing features: *Pseudocyphellaria gretae* is an endemic species forming irregular rosettes on bark and having broadly rounded to sublinear lobes with entire to incised, crenulate, often densely isidiate margins. The upper surface is densely to sparsely tomentose (Fig. 74B), often with granular to coralloid tomentose isidia spreading as a thick, diffract crust. It has a white medulla, a green photobiont, and whitish, densely tomentose lower surface with minute, scattered, white to pale yellow pseudocyphellae. Apothecia are very rare, marginal, and laminal, distinctly pedicellate with ragged, isidiate margins and a tomentose, areolate-scabrid exciple, concolorous with thallus. Spores are brown, thickened 1-septate to 3-septate. There is no detectable chemistry.

Variation: *Pseudocyphellaria gretae* shows some variation in lobe morphology in the degree of development of tomentum, and in the numbers and position of the isidia. All specimens examined were tomentose to some extent and all were isidiate. Well-developed specimens from beech forest are usually thickly tomentose and richly isidiate, and these characters also seem to correlate with medium to high rainfall. Specimens from drier areas are often thinner, cracked or torn and of much smaller size. *Pseudocyphellaria gretae* is distinguished from *P. pubescens* by the marginal and laminal isidia, the epruinose apothecial discs which are red-brown and not black, by the white pseudocyphellae, and by the lack of acetone-soluble metabolites detectable on t.l.c. These characters also distinguish *P. gretae* from *P. fimbriata* which has marginal, tomentose phyllidia, coriaceous, irregularly elongate-laciniate lobes which are not tomentose, a dark brown lower surface with large white pseudocyphellae, and a two-hopane chemistry.

Specimens collected by Richard Helms (1842–1914) from near Greymouth (H-NYL, W) are annotated in Nylander's hand 'Sticta obvoluta Ach.' under which name it was recorded in Nylander (1888*b*:36–7), Müller Argoviensis (1894), and Hellbom (1896– as *Lobaria obvoluta*).


Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
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Campbell I
Macquarie I
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42°
44°
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166°
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170°
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100
km

Fig. 75 Distribution of *Pseudocyphellaria gretae*.

As *Pseudocyphellaria obvoluta* it is recorded by Martin (1966, 1969*a*) and Martin & Child (1972), though in this last account, the plant referred to is obviously *P. pubescens*.

Distribution: (Fig. 75) North I., from Raglan Harbour (Lat. 36°50′S) to Wellington, and in South I., from Nelson to Fiordland and eastwards from north Canterbury near the Lewis Pass to Invercargill. Also on Stewart I., from Oban to Port Pegasus, mainly lowland to subalpine, sea-level to 1200 m.

Habitat ecology: Pseudocyphellaria gretae is best developed in areas of high rainfall and is especially well-developed on beech trees near the Lewis Pass where very large rosettes are often found on trunks. It appears to prefer moist, cool, humid conditions in moderate but not dense shade, though smallish specimens on scrub can withstand full sunlight. *P. gretae* is known from the following phorophytes: *Dacrycarpus dacrydioides*, *Griselinia littoralis*, *Leptospermum scoparium*, *Nothofagus fusca*, *N. solandri* var. *cliffortioides*, *N. menziesii*, *Podocarpus totara*, *Pseudopanax crassifolius*, and *Sphaeropteris medullaris*. *P. gretae* associates with the following lichens: *Coccocarpia palmicola*, *Degelia durietzii*, *Leioderma amphibolum*, *L. sorediatum*, *Lobaria adscripta*, *Menegazzia caliginosa*, *M. lucens*, *Nephroma australe*, *Phlyctella megalospora*, *Parmelia testacea*, *P. tenuirima*, *Pseudocyphellaria billardierei*, *P. fimbriata*, *P. glabra*, *P. pickeringii*, *P. pubescens*, *P. multifida*, *P. homoeophylla*, *Sphaerophorus melanocarpus*, *S. ramulifer*, *S. tener*, *Usnea capillacea*, and *U. xanthophana*.

Specimens examined: 40.

26. **Pseudocyphellaria haywardiorum** D. Galloway, **sp. nov.** **Fig. 76**

Diagnosis: Pseudocyphellariae bartlettii similis sed thallus supra punctulatus non faveolatus, subtus pseudocyphellis niveis, 0·1–2 mm latis. Sporae dilute fuscescentes, (27·5–)30–32(–34) × 6–7 μmm. Medulla K–, KC–, C–, Pd–. Typus: New Zealand, North Island, South Auckland, Red Mercury Island, on tea tree (*Leptospermum*) bark, August 1971, *B. W. & G. C. Hayward* H 40·4 (AK 161261! – holotype). [t.l.c.: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol].

Named for Bruce and Glenys Hayward (Lower Hutt) for their collections of, and researches into, the lichens of the offshore islands of northern New Zealand.

Morphology: Thallus ± orbicular, 3–7(–12) cm diam., corticolous, loosely to firmly attached from margins to centre, or margins ± ascending. *Lobes* ± rounded to irregularly laciniate, 2–10(–20) mm wide, 4–25 mm long, discrete, contiguous or ± complex-imbricate and clustered. *Margins* sinuous, ± ascending, very irregular, delicately to coarsely crenate-lacerate, slightly thickened below, or with clustered soredia and ± grey-white, erose below. *Upper surface* dark grey-blue or glaucous-blue to blue-black, darker at lobe apices or with a livid brownish tinge when moist, olivaceous-brownish to glaucous-yellowish or isabelline, dark greyish at margins when dry, plane or shallowly undulate, ± wrinkled-faveolate at apices, elsewhere conspicuously punctate-impressed, here and there with minute, pale buff papillae (× 10 lens), matt, smooth or appearing minutely arachnoid in parts, rather coriaceous when dry, soft and flabby when moist, sorediate, maculate, without phyllidia or pseudocyphellae. *Maculae* minute, scattered, irregular, whitish buff, most noticeable and in reticulate patterns towards lobe apices, occasionally more extensive photobiont-free patches centrally. *Soredia* coarsely granular to crowded-pseudoisidiate (× 10 lens), scattered in efflorescent clusters, 0·5 mm diam., often dense and spreading, delimited in round to irregular, laminal soralia, or in ± sinuous, linear, marginal soralia, or ± coalescing and forming broad areas of sorediate to pseudoisidiate crust, soredia dark brownish blue, glaucous-greyish, often eroding white. *Medulla* white. *Photobiont Nostoc*. *Lower surface* ± bullate or irregularly undulate-wrinkled, pale buff or brownish and ± glabrous in a narrow, marginal zone, elsewhere evenly and often densely tomentose, red-brown to brown-black, tomentum short and velvety near margins, long and woolly centrally. *Pseudocyphellae* white, conspicuous, well delimited from tomentum, common centrally, rare marginally, round to irregular, 0·1–2 mm diam., with a conspicuously raised, pale-buff, glabrous margin, decorticate area concave to convex, granular. *Apothecia* rare or absent, marginal and laminal, solitary or in groups (2–7), sessile, constricted at base to subpedicellate, rounded, irregular or ±

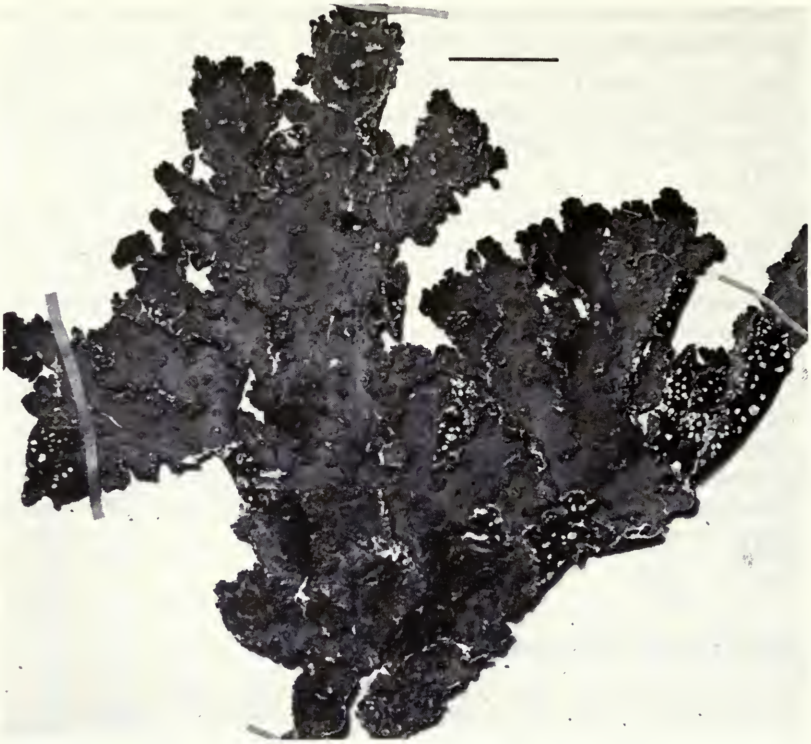


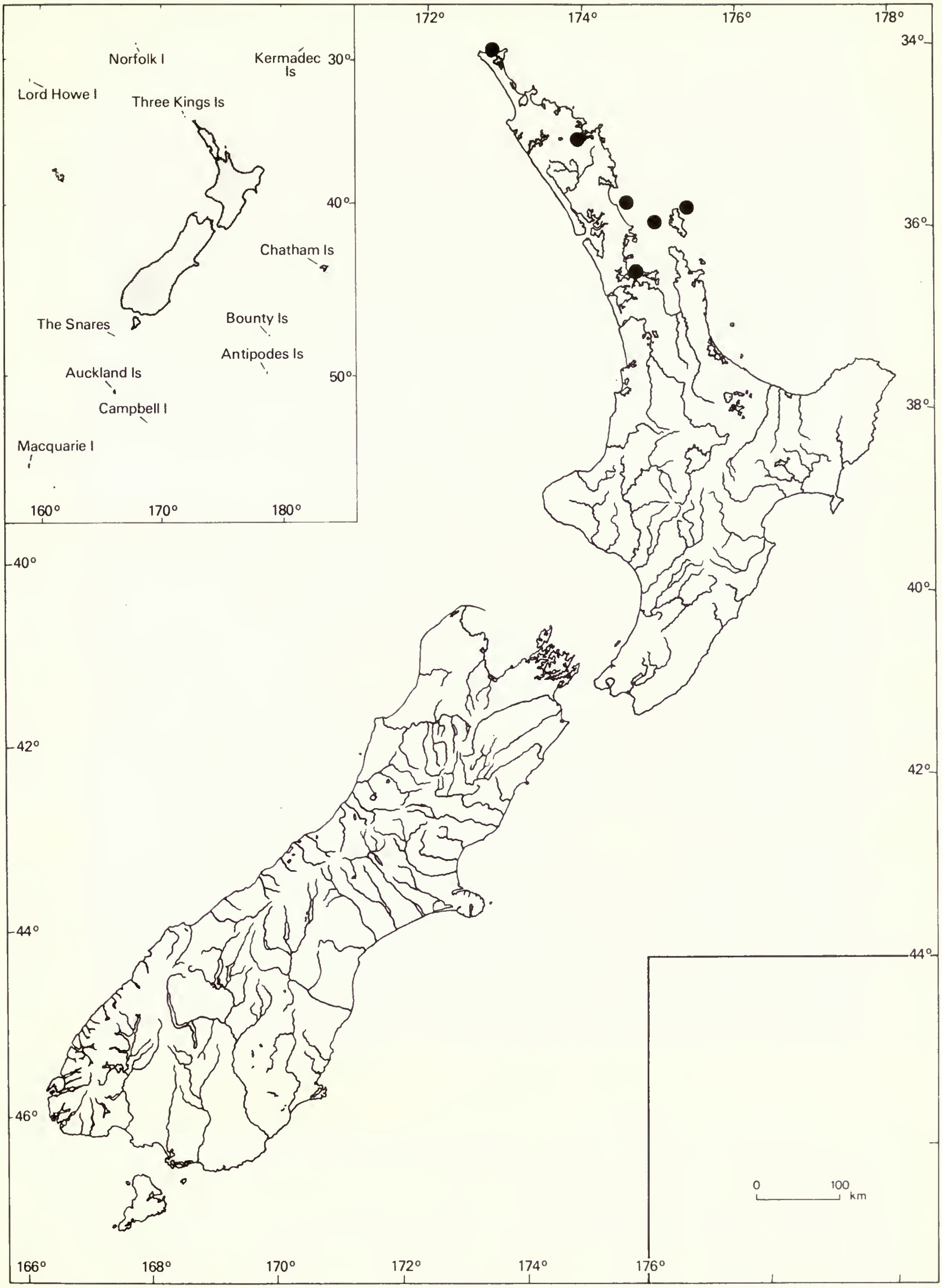
Fig. 76 *Pseudocyphellaria haywardiorum*. Holotype (AK). Scale = 1 cm.

compressed-distorted through mutual pressure, (0·1–)0·5–2·5(–3) mm diam, concave at first, becoming plane to convex at maturity, disc pale yellow or orange-brown to dark red-brown, shining at first, then matt and slightly roughened with age, epruinose, *exciple* pale-buff to brownish, translucent when moist, finely to coarsely scabrid-verrucose.

Anatomy: *Thallus* 220–460(–550) µm thick. *Upper cortex* 34–45 µm thick, cells 4·5–9 µm diam., outermost 10–12 µm yellow-brown to red-brown, remainder hyaline to pale straw. *Photobiont layer* 45–75 µm thick, with prominent dark red-brown hyphae between bundles of photobiont, and running from cortex to medulla, *photobiont Nostoc*. *Medulla* colourless, 90–360 µm thick, hyphae to 4·5 µm diam. *Lower cortex* 2–3 rows of round to irregular thick-walled cells, outermost layer dark red-brown, inner two rows colourless to pale straw, 4·5–11·5 µm diam. *Tomental hairs* yellow-brown to red-brown, 45–230 µm long, in fascicles. *Apothecia: Exciple* cellular, 45–110 µm thick, without photobiont, outermost layers pale red-brown, remainder colourless to straw-yellow. *Hypothecium* (30–)45–65 µm thick, dilute yellow-brown, unchanged in K. *Thecium* colourless, 75–95 µm tall, *epithecium* 18–23 µm thick, clear yellow-brown to red-brown, unchanged in K. *Asci* 55–70(–80) × 13–15(–20) µm. *Ascospores* fusiform-ellipsoid, apices pointed, yellow-brown, 1-septate, unthickened, (27·5–)30–32(–34) × 6–7 µm [spore measurements taken from a specimen from Rangitoto I., collected by *H. H. Allan* (CHR)].

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol. [Code A of Wilkins & James (1979)].

Distinguishing features: *Pseudocyphellaria haywardiorum* is an Australasian sorediate species having ± rounded to irregularly laciniate lobes with coarsely granular to pseudoisidiate (× 10 lens) laminal and marginal soralia, and a conspicuously punctate-impressed upper surface. Neither surface depressions nor soralia are arranged in a reticulate pattern. It has a white


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
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Antipodes Is
Auckland Is
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170°
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Fig. 77 Distribution of *Pseudocyphellaria haywardiorum*.

medulla, a blue-green photobiont, and prominent large, white pseudocyphellae, well delimited from the densely and evenly tomentose, red-brown to brown-black lower surface. It has a two-hopane chemistry [code A of Wilkins & James (1979)].

Variation: This characteristic, northern coastal forest species is still rather poorly known and still rather seldom collected, and the 15 specimens examined in this study show little variation in most external characters except lobe configuration (broadly rounded to irregularly laciniate). I have not studied the species in the field so can report little about either its morphological variation or its habitat ecology. *P. haywardiorum* is distinguished from *P. intricata* by the punctate-impressed upper surface and the ± bullate lower surface with its prominent, large, raised pseudocyphellae, characters which also separate it well from *P. argyracea*, a related isidiate species. It is also distinct from *P. bartlettii* in lobe configuration (*P. bartlettii* has broad, rounded lobes and always forms neat rosettes), soralium morphology, and in chemistry, *P. bartlettii* being C+ rose (cortex) and K+ yellow (medulla) while *P. haywardiorum* is negative to both spot tests. *P. bartlettii*, which is also much thinner in texture, also lacks the conspicuous punctate-impressed upper surface of *P. haywardiorum* and is instead, weakly to strongly reticulate-faveolate. *P. haywardiorum* is also superficially similar to *Lobaria scrobiculata*, but the latter does not have pseudocyphellae and it has a distinctive and different chemistry [medulla K+ orange-red, C± rose, Pd+ orange. Constictic, norstictic, stictic, and usnic acids, and scrobiculin] and, moreover, is scabrid-areolate near the margins which are never maculate. Apothecia appear to be rather rarely developed in *P. haywardiorum*, only two of the specimens examined were fertile and two others were infected with a lichenicolous fungus.

Distribution: (Fig. 77) In coastal forest from Radar Bush, North Auckland to Rangitoto I., near Auckland city. Absent on the Three Kings Is, but present on the following northern offshore islands: Poor Knights Is, Lady Alice I., Hen I., Little Barrier I., Rakitu I., and Red Mercury I. It has an altitudinal range from sea-level to 240 m. In some previous accounts (Hayward & Hayward, 1978, 1980, 1982*a*, 1982*b*, 1984) the species is recorded as *P. granulata*.

Habitat ecology: *Pseudocyphellaria haywardiorum* is an epiphyte of both bark and twigs of the following phorophytes in northern coastal forest: *Cordyline australis*, *Kunzea ericoides*, and *Metrosideros excelsa*. It is known also from *K. ericoides* in grassland. It is one of a group of northern species (*P. aurata*, *P. bartlettii*, *P. carpoloma*, and *P. poculifera* are others) closely associated with *Cordyline*, *Metrosideros*, and *Leptospermum* in lowland and primarily coastal habitats north of lat. 37°S.

Specimens examined: North Island. North Auckland: Radar Bush, 7 May 1976, *J. K. Bartlett* 24641 (Herb. Bartlett, BM) – also collections (unnumbered) from 1 & 2 January 1980, *J. K.* Bartlett (Herb. Bartlett, BM); Bay of Islands, Waiparo Bay, *B. W. & G. C. Hayward*, January 1980 (AK 161552); Poor Knights Islands. Tawhiti Rahi, September 1980, *B. W. Hayward* (AK 164496, BM); Lady Alice Island, *B. W. & G. C. Hayward* (AK); Little Barrier Island, *B. W. & G. C. Hayward* L33, L20 (AK); Rakitu Island, January 1981, *B. W. Hayward* (AK 164490); Rangitoto Island, 24 April 1927, *G. E. & Greta Du Rietz* 2673: 3 (UPS); 13 April 1936, *H. H. Allan* (BM, CHR); January 1935, *H. H. Allan* (BM, CHR); *L. H. Millener* (BM, CHR).

27. Pseudocyphellaria homoeophylla (Nyl.) Dodge **Fig 78**

in *Nova Hedwigia* **19**: 489 (1971). – *Sticta homoeophylla* Nyl. in *Flora, Jena* **50**: 439 (1867). – *Lobaria homoeophylla* (Nyl.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21**(3/13): 39 (1896). Type: New Zealand, sine loco (prob. Wellington), 1867, *C. Knight* (H-NYL 33464! – holotype; WELT, Herb. Knight Vol. 36A, p. 9! – isotype).

Sticta amplificata Zahlbr. in *Denkschr. Akad. Wiss. Wien math.-naturwiss. Kl.* **104**: 287 (1941). Type: New Zealand, Ohakune, *L. B. Moore* ZA 167 (W 2506! – holotype; CHR 374654! – isotype).

Morphology: *Thallus* orbicular to spreading, often forming extensive swards, 10–20(–50) cm diam., loosely adnate centrally, margins free, projecting outwards or ± ascending, corticolous, saxicolous or terricolous. *Lobes* very variable, ± linear-laciniate, di- or trichotomously

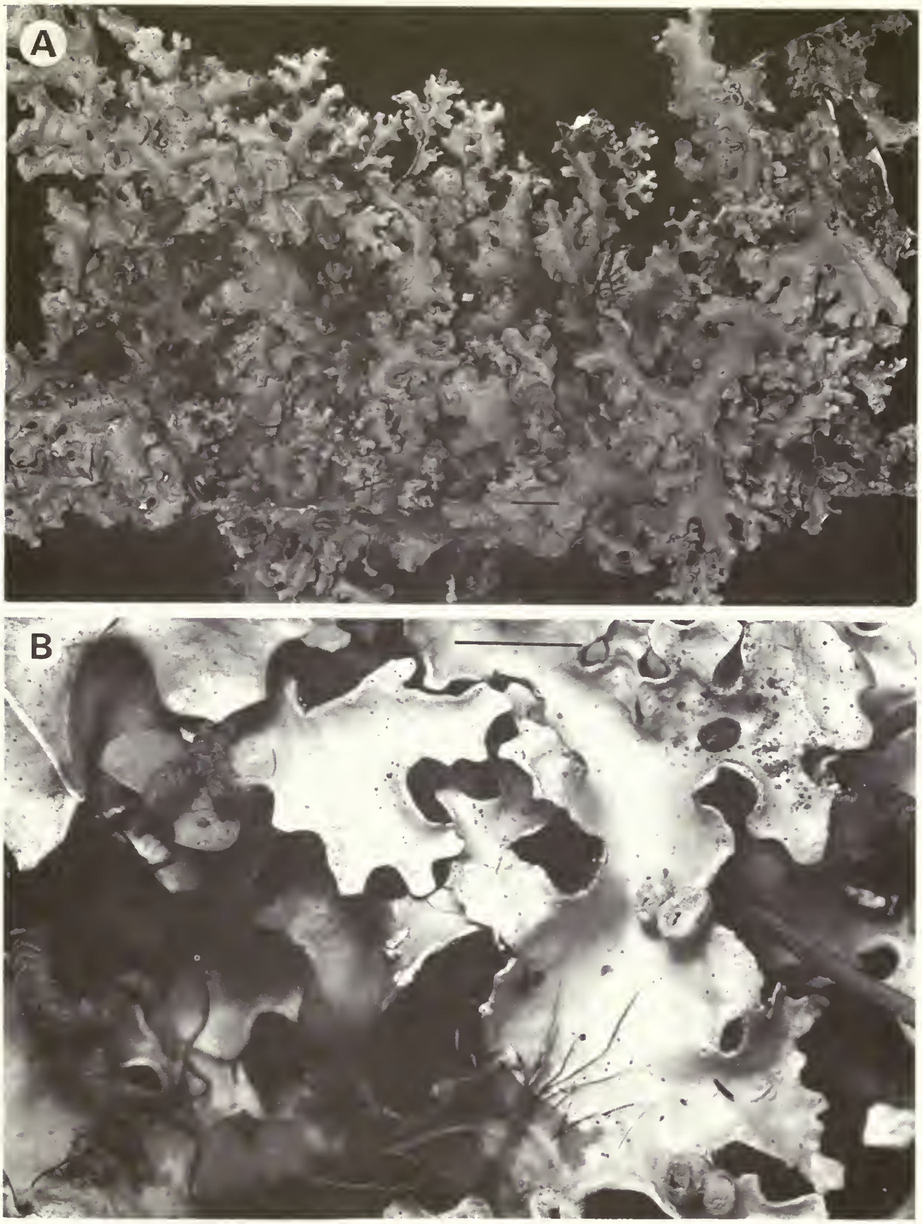


Fig. 78 *Pseudocyphellaria homoeophylla*. Nina Valley, *Galloway* (CHR 374645). A. Scale = 1 cm. B. Scale = 5 mm.

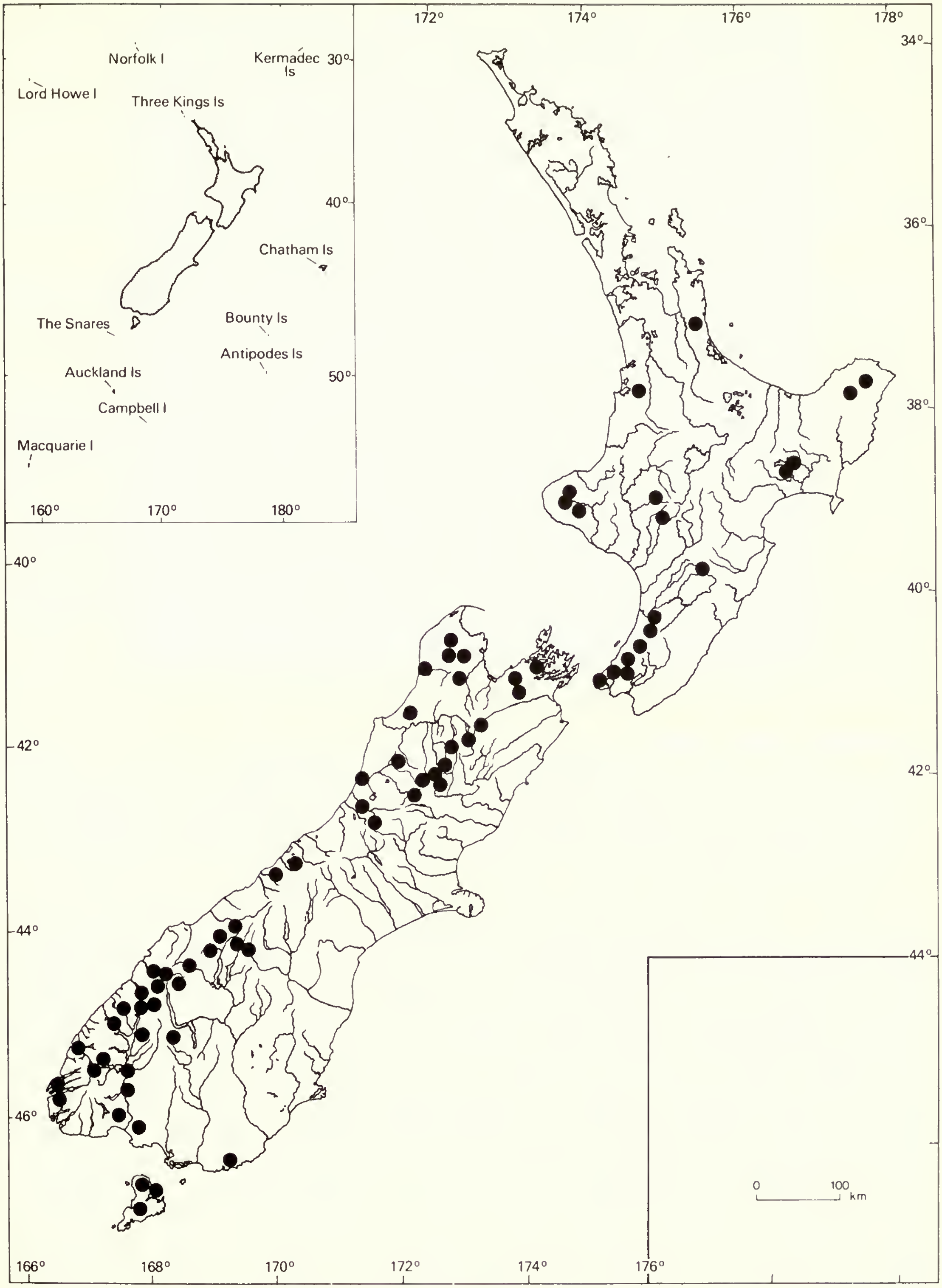
branched at apices, complex-imbricate centrally, 2–5(–10) mm wide, occasionally to 25 mm wide, and rarely to 40 mm wide centrally (in *S. amplificata*), and to 12 cm long. *Margins* entire, sinuous, shallowly scalloped or notched at apices, smoothly rounded and ± markedly thickened and sometimes ridged below, without pseudocyphellae, sinuses semicircular. *Upper surface* bright lettuce-green when wet, pale greenish grey when dry, becoming yellowish buff on prolonged storage in herbarium, smooth, matt, coriaceous, undulate, shallowly wrinkled or pitted, occasionally with a crazing of fine black lines, or obscurely ridged, never reticulate-faveolate, without isidia, maculae, pseudocyphellae or soredia. *Medulla* white. *Photobiont* green. *Lower surface* pale yellowish buff to brown at margins, red-brown to black centrally, shallowly wrinkled-plicate or pitted, internal cephalodia visible as scattered, hemispherical, wrinkled swellings 1–2 mm diam., patchily tomentose from margins to centre or with extensive marginal and central glabrous areas, tomentum short, entangled, white or buff to ± blackened. *Pseudocyphellae* common, conspicuous, white, round to irregular, 0·1–1 mm diam., ± strongly excavate, crateriform, with strongly defined, raised margins. *Apothecia* marginal or submarginal, most common towards lobe apices, 1–4(–6) mm diam., rounded, concave at first becoming shallowly undulate with age, pedicellate to ± sessile, disc pale to dark red-brown, ± blackened with age, matt, epruinose, margins conspicuously denticulate or striate to ± stellate, pale buff, translucent when wet, exciple translucent when wet, pale buff or pinkish or creamish when dry, thickly arachnoid at first and obscuring disc for a time after emergence with a thick plug, becoming coarsely areolate-scabrid with age and projecting from margins at maturity as a stellate fringe. *Pycnidia* submarginal, marginal (often in lines) or scattered on upper surface, hemispherical, minute, 0·2 mm diam. or less, often eroded and leaving shallow pits, commonly clustered near lobe apices.

Anatomy: *Thallus* 180–260 (to 360 at margins) μm thick. *Upper cortex* 45–54(–64) μm thick, upper zone of 15–20 μm appearing ± fibrous, pale straw-coloured or yellow-brown, of necrotic, ± compressed cells, lower zone abutting photobiont layer, colourless, of round to irregular, thin-walled cells in a pseudoparenchyma, cells 4·5–15 μm diam. *Photobiont layer* 18–27 μm thick, *photobiont* green, cells rounded, 7–9 μm diam. *Medulla* 90–200 μm thick, hyphae loosely interwoven, 2–3 μm diam., encrusted with granular crystals and appearing ± greyish olive. *Lower cortex* 27–34(–45) μm thick, outer 10–12 μm pale to dark red-brown, inner zone adjoining medulla, hyaline to pale straw-coloured of thick-walled round to irregular, ± isodiametric cells in 6–8 rows, walls 2–2·5 μm, lumina 2–3 μm diam. *Tomental hairs* septate, red-brown, 7–9 μm thick, septate, constricted at septa, locules short, single or in scattered fascicles 4-8-together, 45–140(–230) μm long. *Apothecia: Exciple* cellular, colourless, 90 μm thick at margins, 180–230 μm thick below disc, cells 10–15 μm diam., thicker in outer parts of tissue, splitting below into large, pyramidal clumps (surface scabrosity) with 1–3 rows of cells extending at margins as short, tomental hairs. *Hypothecium* 45–75 μm thick, very pale yellow or orange-brown, dense. *Thecium* 80–90(–100) μm tall, colourless, yellow-brown towards tips of paraphyses; *epithecium* 11–22 μm thick, pale yellow-brown, slightly granular, colour dissolving in K. Medulla and a narrow photobiont zone (30 μm) between hypothecium and exciple. *Asci* 78–85 × 18–20·5 μm. *Ascospores* fusiform-ellipsoid, apices rounded or pointed, straight or curved, pale straw, 1-3-septate, not thickened, 25–32 × 7–9 μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol, norstictic, stictic, cryptostictic, constictic, methylstictic, hypostictic, and hyposalazinic (tr.) acids, and ± usnic acid (Elix, 1986).

Distinguishing features: *Pseudocyphellaria homoeophylla* is an endemic species having di- or trichotomously branching, ± linear-laciniate lobes, with entire, sinuous margins (Fig. 78B), lacking soredia, isidia, phyllidia, or pseudocyphellae. The upper surface is glabrous, smooth to shallowly wrinkled or pitted, never faveolate, ± coriaceous. It has a white medulla, a green photobiont, and a red-brown to black lower surface with rather patchy tomentum and with numerous, conspicuous, white pseudocyphellae. Apothecia are sparse to moderately common, mainly marginal and towards apices, the exciple prominent, coarsely areolate-scabrid, buff to pinkish, often ± stellate-fimbriate at margins. Spores are fusiform-ellipsoid, pale straw-coloured, 1-3-septate. The chemistry comprises two main hopanes [Code A of Wilkins & James (1979)] with the addition of stictic acid metabolites and usnic acid, the last of which gives the thallus a yellowish tinge.

Variation: *Pseudocyphellaria homoeophylla* varies most widely in the width of its lobes, particularly exuberant forms, especially in the northern part of its range, having very broad lobes [25–40 mm wide as in *Sticta amplificata*] while most southern collections are narrower 2–10 mm wide. The entire, sinuous, somewhat scalloped margins, which are devoid of asexual propagules, distinguish this species from the two most closely related taxa, the isidiate *P. glabra*


Norfolk I
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Chatham Is
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Fig. 79 Distribution of *Pseudocyphellaria homoeophylla*.

and the marginally phyllidiate *P. corbettii*, both of which have the same chemistry as *P. homoeophylla*. It is distinct from the South American subantarctic species *P. freycinetii* which has more irregular, indented-lacerate margins and much larger, broader (0·5–4·5 cm wide), shorter, thinner, and more papery lobes (Galloway & James, 1986).

Specimens recorded in Zahlbruckner (1941) as *Sticta dissimulata* (p. 283) are referable to *P. homoeophylla*, as are several specimens recorded as *Sticta freycinetii* (ZA 407 & 667; V 206; V 60; V 61 –W!), or as *Sticta sinuosa* (W 10; ZA 161 & 666).

Pseudocyphellaria homoeophylla is the counterpart primary species to the isidiate *P. glabra*, the two taxa forming a species pair. It is, however, known only from New Zealand and does not share the same austral range of distribution as *P. glabra*.

Distribution: (Fig. 79) North I., south of lat. 37°S on most mountain ranges, on both east and west coast to Wellington (Akatarawa Range), and in South I., from Nelson and Marlborough Sounds close to and west of the Main Divide to Fiordland, also in the Catlins (Southland) and in Stewart I., lowland, montane to subalpine, sea-level to1440 m.

Habitat ecology: *Pseudocyphellaria homoeophylla* is primarily a rain-forest species and is best developed in beech (*Nothofagus*) forest close to the Main Divide in South I. It is especially common both as an epiphyte and as a forest floor species where it competes successfully with bryophytes (in some areas it may form extensive swards) in mid-altitude forests (200–600 m) and in areas dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*) it is the dominant epiphyte up to treeline where increased light and exposure allows other species of *Pseudocyphellaria* to proliferate. Its often great size and luxuriant development, along with *P. colensoi* and *P. coronata*, make it one of the most prominent of cryptogamic epiphytes in New Zealand beech forest, and it undoubtedly contributes substantially to the forest biomass. Apart from species of beech (*N. fusca*, *N. menziesii*, *N. solandri*), it is known from the following phorophytes: *Agathis australis*, *Dacrycarpus dacrydioides*, *Libocedrus bidwillii*, *Myrsine divaricata*, *Pseudopanax*, *Quintinia serrata*, and *Weinmannia racemosa*.

Specimens examined: 140.

28. **Pseudocyphellaria hookeri** (Church. Bab.) D. Galloway & P. James **Fig. 80**

in *Lichenologist* **12**: 299 (1980). – *Sticta hookeri* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 282 (1855). – *Stictina hookeri* (Church. Bab.) Nyl., *Syn. meth. lich.* **1**(2): 336 (1860). – *Saccardoa hookeri* (Church. Bab.) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Cyanisticta hookeri* (Church. Bab.) Gyelnik in *Feddes Reprium Spec. nov. veg.* **29**: 2 (1931). Type: New Zealand, Bay of Islands, *J. D. Hooker* (BM! – lectotype).

Morphology: *Thallus* orbicular, ± rosette-forming, loosely attached centrally, margins free, ascending, 5–10(–15, rarely to 22) cm diam., corticolous. *Lobes* broadly laciniate, ± rounded at apices, 0·5–2·5 cm diam., ± discrete or subimbricate at apices, complex-imbricate centrally, plane or shallowly convex towards apices, ± shallowly concave centrally. *Margins* entire, sinuous, shallowly crenate to irregularly convolute or sublobulate, shining, often suffused brownish, slightly thickened below or ± inflated, with occasional minute, punctiform, pale yellow pseudocyphellae. *Upper surface* dark slate-blue or blue-grey, suffused red-brown in parts especially towards margins when moist, glaucous-grey to red-brown when dry, strongly reticulate-faveolate, faveolae weakly to strongly defined, shallow or deep, interconnecting ridges rather short, smoothly rounded to sharply delimited, matt to glossy, smooth or wrinkled, without soredia, isidia, phyllidia or pseudocyphellae. *Maculae* common, effigurate, whitish to pale buff, scattered, or forming an irregular reticulum, larger photobiont-free areas visible as whitish or pale buff spots or blotches. *Medulla* white. *Photobiont Nostoc. Lower surface* pale buff or whitish at margins, darker centrally, irregularly wrinkled-bullate especially at lobe apices, ± glabrous at margins, elsewhere ± uniformly short, stiff, tomentose, tomentum brownish often in discrete bundles. *Pseudocyphellae* minute, common, on raised, nodular to ± elongate verrucae, margins concolorous with lower cortex, conspicuous, decorticate area often reduced to a thin slit or scarcely apparent, pinprick-like, very pale yellow or whitish. *Pycnidia*

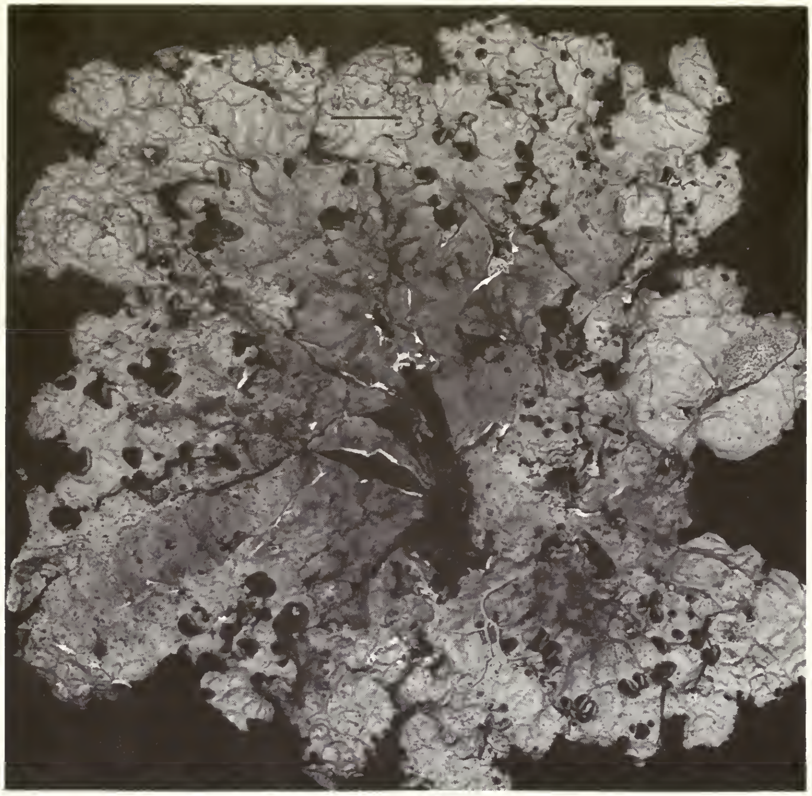
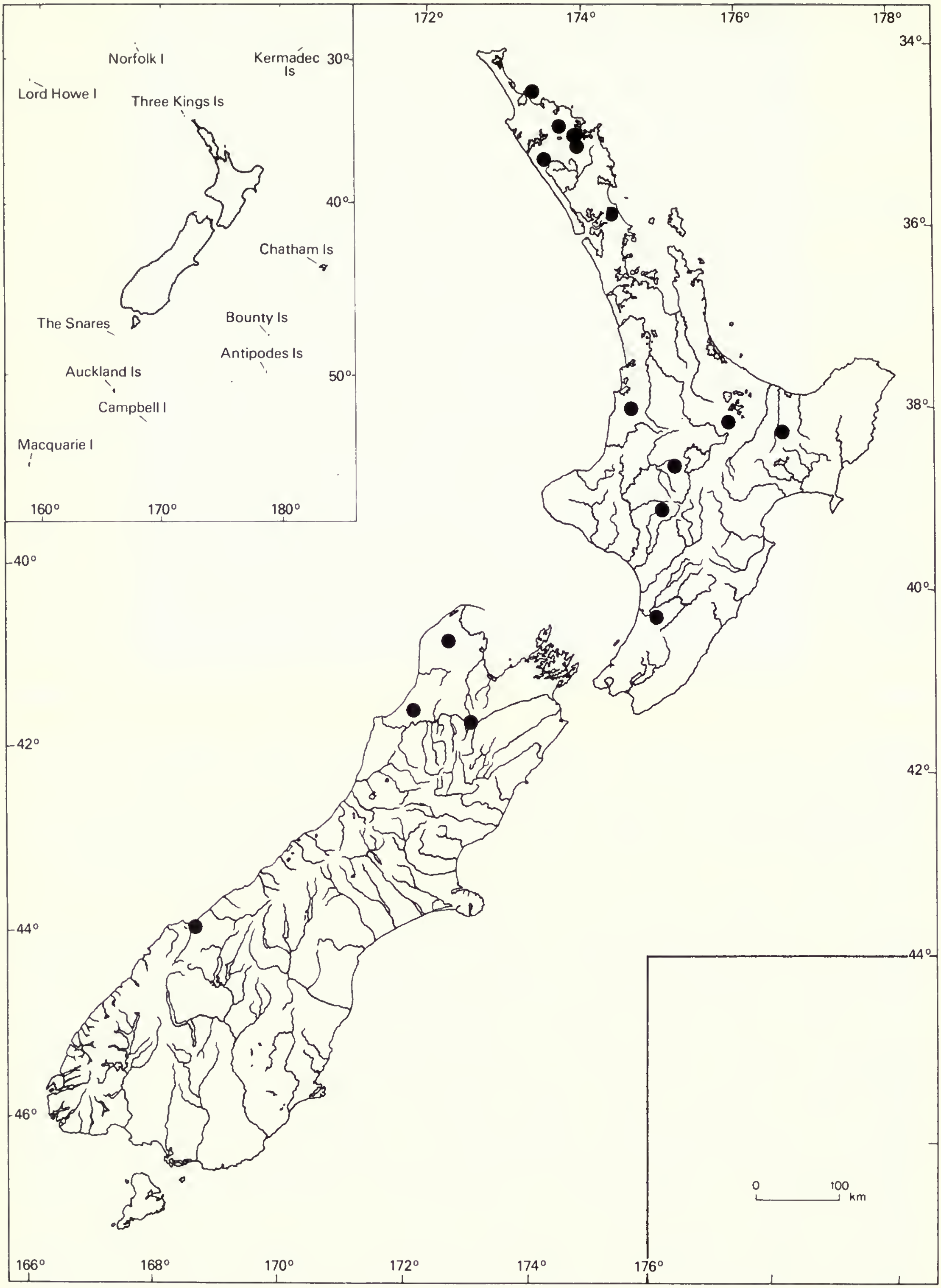


Fig. 80 *Pseudocyphellaria hookeri*. Mangaotaki Valley, Pio Pio, *Galloway* (CHR 375877). Scale = 1 cm.

numerous, scattered, marginal and laminal, or in rows on thalline ridges, papillate, 0·1–0·4 mm diam., ostiole red-brown, punctate. *Apothecia* sessile to pedicellate, sparse to frequent, round to irregular, 1–8 mm diam., concave at first becoming plane to irregularly convex-undulate with age, disc dark brown to black, matt or minutely granular-papillate, epruinose, margins concolorous with thallus, crenate-striate, involute when young, exciple concolorous with thallus, smooth and ± shining to wrinkled or faveolate, occasionally ± scabrid-areolate (× 10 lens), in places minutely tomentose, tomentum thin, brownish.

Anatomy: *Thallus* 100–230(–320) μm thick. *Upper cortex* 22–27 μm thick, dilute straw-yellow above, colourless below, cells 4 μm diam. or less. *Photobiont layer* 36–55(–64) μm thick, in irregular clumps, *photobiont Nostoc*, cells to 11 μm diam. *Medulla* 45–200 μm thick, colourless, hyphae to 4·5 μm diam. *Lower cortex* 11·5–15·5 μm thick, dilute yellow-brown, dissolving in K, cells 4·5 μm diam. or less. *Tomental hairs* colourless to pale brown, 45–230 μm long, in scattered fascicles. *Apothecia: Exciple* colourless, 73–110 μm thick, irregularly scalloped at margins, cells thick-walled, 4·5–12 μm diam. *Hypothecium* dilute yellow-brown, intensifying in K, 40–45 μm thick. *Thecium* colourless, 100–112 μm tall; *epithecium* granular, not dissolving in K, 7–14 μm thick, dark olive brownish turning violet-purple in K. *Asci* 63–76 × 15·5–18 μm. *Ascospores* smoky olive-brown, thickened 1-septate to 3-septate, broadly fusiform, straight or curved, septum of thickened 1-septate spores 4·5–7 μm thick, contents granular, (18–)23–27 × 7–9 μm.

Chemistry: Methyl evernate, tenuiorin, two unidentified depsides (tr.), methyl lecanorate, methyl gyrophorate, evernic acid (tr.), gyrophoric acid, hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α-acetoxyhopane-7β, 22-diol (tr.), norstictic (tr.), stictic, cryptostictic, constictic, and hypostictic acids (tr.), and traces of pulvinic acid, pulvinic dilactone, and calycin.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Lord Howe I
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Fig. 81 Distribution of *Pseudocyphellaria hookeri*.

Distinguishing features: *Pseudocyphellaria hookeri* is an endemic, rosette-forming species having broadly laciniate lobes with entire, sinuous, crenate to irregularly convolute-sublobulate margins. The upper surface is strongly reticulate-faveolate, with whitish or buff maculae but without soredia, isidia, phyllidia or pseudocyphellae. It has a white medulla, a blue-green photobiont, and a wrinkled-bullate, buff or brown, tomentose lower surface with scattered, minute, whitish or pale yellow pseudocyphellae. Apothecia common, sessile to subpedicellate, disc black, granular-roughened, epruinose, exciple concolorous with thallus. Epithecium granular, olive, turning violet-purple in K. Spores olive-brown, thickened 1-septate to 3-septate. It has a complex chemistry containing gyrophoric acid (cortex C+ red), depsidones, hopane-6α, 7β, 22-triol, and stictic acid metabolites.

Variation: *Pseudocyphellaria hookeri* is a species of uniform morphology throughout its range. It is distinguished from *P. durietzii* by the blue-green photobiont and the brown tomentum of the lower surface; however, the two species are closely similar morphologically and chemically and photosymbiodemes of the two species are known. *P. montagnei* is similar chemically, but differs in the thinner, more fragile, less faveolate lobes, in the closely appressed habit (*P. hookeri* is usually only centrally attached and is free and ± subascendent at the margins), the pale buff sparsely tomentose lower surface with pale yellowish insignificant sparse pseudocyphellae, and the laminal phyllidia and phyllidiate apothecial margins.

Distribution: (Fig. 81) Mainly a northern species in North I., from lat. 34°50′S at Cape Karikari, to the Manawatu, throughout. Rare in South I., (north-west Nelson and Jackson Bay), mainly lowland to subalpine, sea-level to 400 m.

Habitat ecology: *Pseudocyphellaria hookeri* is primarily a northern species, characteristic of cool, moist, humid habitats (gullies, stream sides, on successional shrubs, or in standing forest or forest remnants), in moderate to deep shade. It is mainly a twig species and is often richly developed on young regenerating *Dacrycarpus dacrydioides*. It is also known from the following phorophytes: *Coprosma* spp., *Leptospermum scoparium*, *Myrtus bullata*, *Podocarpus hallii*, *Salix*, *Weinmannia racemosa*, and *W. silvicola*.

Specimens examined: 30.

29. **Pseudocyphellaria intricata** (Delise) Vainio **Fig. 82A, B**

in *Hedwigia* **37**: 35 (1898). – *Sticta intricata* Delise in *Mém. Soc. linn. Normandie* **2**: 96 pl. 7 fig. 33 (1825). – *Stictina intricata* (Delise) Nyl., *Syn. meth. Lich.* **1**(2): 334 (1860). – *Cyanisticta intricata* (Delise) Gyelnik in *Lilloa* **3**: 76 (1938). Type: Île de Bourbon (Réunion), *Bory de St-Vincent* (PC-LENORMAND! – lectotype) [see note 1].

Sticta thouarsii Delise in *Mém. Soc. linn. Normandie* **2**: 90 pl. 8 fig. 29 (1825). – *Stictina intricata* var. *thouarsii* (Delise) Nyl., *Syn. meth. lich.* **1**(2): 335 (1860). – *Pseudocyphellaria intricata* var. *thouarsii* (Delise) Vainio in *Hedwigia* **37**: 35 (1898). – *Stictina thouarsii* (Delise) Hav., *Lich. Exs. Norveg.* 430 (1913). – *Sticta intricata* f. *thouarsii* (Delise) Zahlbr., *Cat. Lich. Univ.* **3**: 388 (1925). – *Cyanisticta thouarsii* (Delise) Räsänen, *Die Flechten Estlands* **1**: 161 (1931). – *Pseudocyphellaria thouarsii* Degel. in *Acta Phytogeogr. Suec.* **7**: 150 (1935). – *Cyanisticta intricata* var. *thouarsii* (Delise) Räsänen in *Revta Univ. Santiago* **21**: 144 (1936). Type: Tristan da Cunha, *Du Petit Thouars* (PC-LENORMAND! – holotype) [see note 1].

Sticta limbata var. *subflavida* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 283 (1855). – *Stictina limbata* var. *subflavida* (Church. Bab.) Nyl. *in* Hue in *Nouv. Archs Mus. Hist. nat. Paris* III, **2**: 300 (1890). Type: New Zealand, Middle Island [South Island], sine loco, *D. Lyall* (BM! – lectotype) [see note 2]. Fig. 82A.

Stictina intricata var. *subargyracea* Nyl., *Lich. Nov. Zel.*: 29 (1888) [qua forma nomen Nyl., *Flora, Jena* **69**: 172 (1886)]. – *Sticta intricata* f. *subargyracea* (Nyl.) Hue in *Nouv. Archs Mus. Hist. nat. Paris* IV, **3**: 90 (1901). Type: New Zealand, sine loco (prob. near Greymouth, Westland), *Helms* 35 (W! – lectotype) [see note 3].

Stictina subcrocea Stirton in *Trans. N.Z. Inst.* **32**: 74 (1900). – *Sticta subcrocea* (Stirton) Zahlbr., *Cat. Lich. Univ.* **3**: 399 (1925). Type: Australia, Queensland, Brisbane, *F. M. Bailey* (BM! – lectotype).

Note 1: Discussing the use of the names *intricata* and *thouarsii*, Jørgensen (1977: 23) states: 'when the two

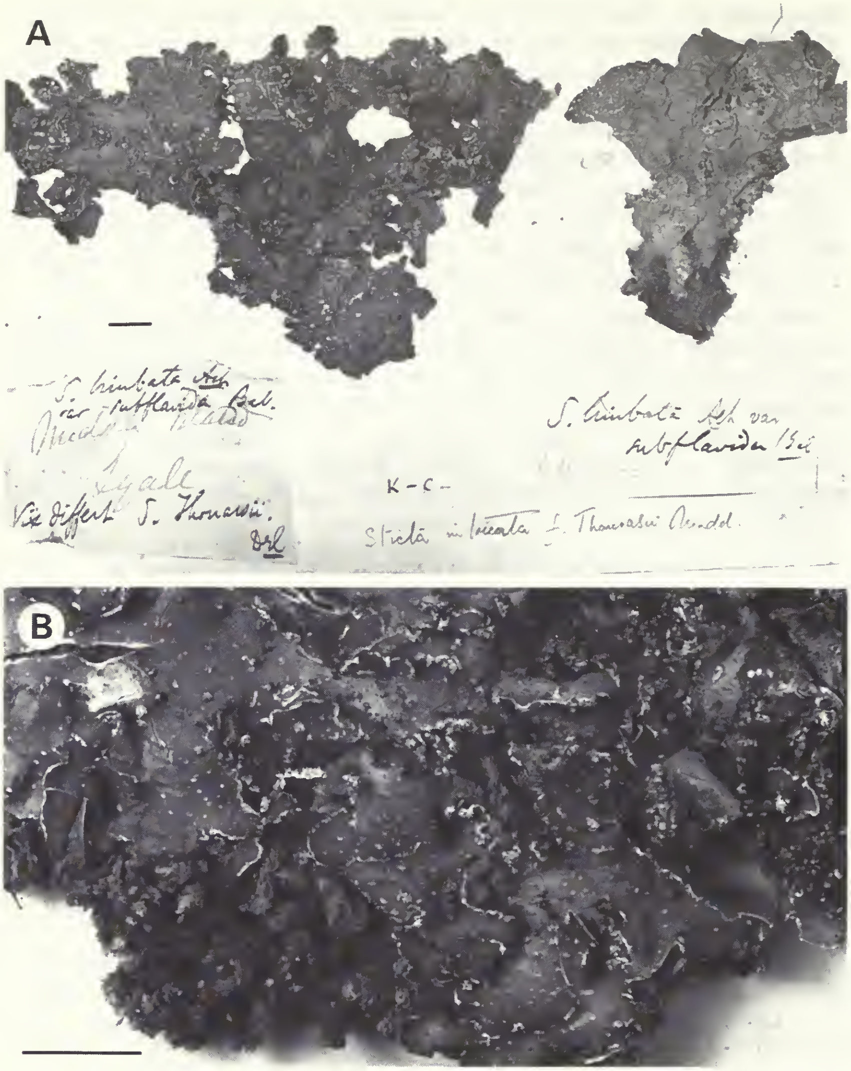

Fig. 82 *Pseudocyphellaria intricata*. A. Lectotype of *Sticta limbata* var. *subflavida* (BM- left). Scale = 1 cm. B. New Zealand, *Helms* 93 (W). Scale = 5 mm.

species are united the correct name is *Pseudocyphellaria intricata* . . . Nylander (1860) united them choosing *intricata* as the species epithet, and he must be followed'.

Note 2: *Sticta limbata* var. *subflavida* Church. Bab.
Babington (1855: 283) states that his taxon scarcely differs from Delise's *Sticta thouarsii*, the colour of the upper surface being 'plus minus fuscoflavescentibus', and further, 'This can hardly be distinguished with safety from the European Lichen. Delise's figure of *S. thouarsii* well represents the ramification, and differs in nothing material except in the white soredia, which are decidedly lead-coloured in the New Zealand plant.' The lectotype of *S. limbata* var. *subflavida* is the left hand specimen on a sheet (BM) containing collections of Lyall, and Colenso (Fig. 82A).

Note 3: *Stictina intricata* var. *subargyracea* Nyl.
The lectotype of this taxon (W) was collected by Richard Helms and is in Herbarium Lojkanum. It consists of three specimens having a mustard-yellow upper surface (of the *subflavida*-type see above), broadly rounded lobes, and mainly laminal soralia, although towards the centre, lobes have linear, marginal soralia. A sheet in WU labelled *Nymphaea intricata* f. *subargyracea* Nyl., has seven specimens of *P.*

intricata collected in New Zealand (probably from near Greymouth in Westland) by Richard Helms. Specimens from both W and WU are growing on *Leptospermum* bark and seem to be from the same collection, having associated with the dominant *P. intricata*, and other lichens, including *Leioderma sorediatum*, *Leptogium cyanescens*, *Pannaria fulvescens*, and *Psoroma leprolomum*.

Morphology: *Thallus* very variable, from narrow-lobed, furcate, to irregularly divided laciniate demes to ± broad-lobed, rounded demes, 2–10(–20) cm diam., rosette-forming to irregularly spreading, closely attached centrally, margins free and often ± ascendent, corticolous, rarely saxicolous. *Lobes* irregularly linear-laciniate, rather ragged, or ± furcate or straplike, or broadly rounded, apices discrete, contiguous or imbricate, 3–10(–25) mm wide, 1–5 cm long, discrete or separate in part from margins to centre, or ± complexly folded centrally with apices only ± discrete. *Margins* rarely entire, usually delicately crenulate to ragged-lacerate, ± ascending, sinuous, often becoming coarsely sorediate and eroding both upper and lower surfaces. *Upper surface* dark glaucous blue-green, olivaceous-glaucous or blue-black suffused brownish or reddish when moist, pale olivaceous greyish, mustard-yellow, grey-brown, or reddish brown sometimes with a lilac tinge when dry, plane, undulate, minutely wrinkled or occasionally subfaveolate to punctate-impressed towards lobe apices, smooth to minutely scabrid in parts (× 10 lens), rarely shining, coriaceous, rarely minutely tomentose in scattered patches near lobe apices, sorediate, without isidia, phyllidia or pseudocyphellae. *Soralia* laminal and marginal, Soredia farinose to coarsely granular, often appearing pseudoisidiate or with clustered, corticate, regenerating lobules, laminal soralia punctiform, or eroding large areas, round to irregular 0·1–3 mm diam., ± flat to distinctly raised, pulverulent, widely scattered, crowded or in lines on shallow ridges near margins, marginal soralia linear, sinuous, eroding lower surface, often ± labriform, soredia white, occasionally brownish or greyish. *Maculae* minute, scattered, irregular, whitish or buff patches (× 10 lens), not in any reticulate pattern, only seen when moist. *Medulla* white. *Lower surface* plane, undulate or irregularly to complexly wrinkled-ridged, pale yellowish or whitish-buff to grey-brown, red-brown or chocolate-brown, rarely with a narrow, glabrous, marginal zone, tomentose from margins to centre, tomentum stiff, silky, even, velvety to woolly-entangled. *Pseudocyphellae* white, rather rare, widely scattered, submerged in tomentum, often absent, round to irregular, 0·2–1·5 mm diam., margins thin, raised, concolorous with lower cortex, decorticate area plane to deeply concave, granular. *Apothecia* very rare, normally absent, laminal, sessile to subpedicellate, 0·2–2 mm diam., rounded, concave at first becoming plane or undulate at maturity, disc pale orange-brown to red-brown, matt or glossy, epruinose, immarginate at maturity, exciple slightly roughened, pale buff or brownish, ± concealing disc at first, excluded at maturity.

Anatomy: *Thallus* 200–370 μm thick. *Upper cortex* 34–40 μm thick, outermost 10 μm pale straw-yellow, cells compressed, remainder colourless, cells 4·5–9 μm diam. *Photobiont layer* 50–90 μm thick, rather variable, *photobiont Nostoc. Medulla* 100–220 μm thick, colourless, hyphae 4·5 μm diam. *Lower cortex* (13–)18–22 μm thick, pale yellow-brown, cells 4·5–9 μm diam., *Tomental hairs* pale yellow-brown to red-brown, to 5 μm diam. and 45–220 μm long, in dense fascicles. *Apothecia: Exciple* colourless, 40–90 μm thick, cells 9–15 μm diam. *Hypothecium* pale yellow-brown or olivaceous-brown 28–45 μm thick. *Thecium* pale straw-yellow, 90–110 μm tall; *epithecium* absent; *paraphyses* densely conglutinate, not much swollen at apices (to 3 μm diam.). *Asci* 76–86 × 15–18 μm. *Ascospores* pale yellow-brown, fusiform-ellipsoid, straight or curved, 3-septate, slightly constricted at septa, contents distinctly vacuolate, (27–)29·5–36·5(–38·5) × 7–9 μm.

Chemistry: Tenuiorin (tr.), methyl gyrophorate (tr.), 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane 15α, 22-diol.

Distinguishing features: *Pseudocyphellaria intricata* is a cosmopolitan species having irregularly laciniate to broadly rounded lobes with sinuous, incised to ± entire, often sorediate margins. The upper surface is plane, undulate to minutely wrinkled or subfaveolate in parts, coriaceous with scattered, erose, laminal and marginal soralia, containing coarsely granular, often pseudoisidiate soredia. It has a white medulla, a blue-green photobiont, and a pale yellow-buff to chocolate-brown tomentose lower surface with occasional to rare, widely scattered, white pseudocyphellae submerged in tomentum. Apothecia generally absent, when present sessile to subpedicellate, the disc pale orange-brown to red-brown, exciple slightly roughened, pale brownish, excluded at maturity. It has a two-hopane chemistry [Code A of Wilkins & James (1979)] with traces of tenuiorin and methyl gyrophorate.

Variation: *Pseudocyphellaria intricata* is a widespread and rather variable species, and lobe morphology, colour of the upper surface, and numbers and position of the soralia all vary, depending on local microhabitat and microclimate conditions. Thick, broad-lobed individuals having a coriaceous, mustard-yellow upper surface and coarse grey-blue, often marginal soralia are common in drier areas and in habitats exposed to relatively high light intensities (Fig. 82A). Specimens from rocks in rough pasture land or near bush margins are most commonly of this form and were referred by Babington (1855) to *Sticta limbata* var. *subflavida*. In wetter, more humid, and more shaded habitats, the upper surface is red-brown to pale grey-brown often with a bluish or lilac tinge, and with ± linear, marginal, and scattered laminal white soralia, often pseudoisidiate at the margins (Fig. 82B). Such forms are typical in forested areas, or from damp, humid scrub in partial shade, and are frequently found growing amongst moss. In some northern collections (especially from the Waiotapu Valley near Lake Rotorua, and also from near Lake Taupo) specimens of *P. intricata* have thin, papery lobes with mainly marginal, sinuous soralia, and are strongly reminiscent of material of this species from Tristan da Cunha, the typical locality of *Sticta thouarsii* Delise (Galloway & James, 1986).

The New Zealand populations, although of variable morphology depending on local ecological conditions, all have a uniform chemistry and are presently regarded as a single variable species. The sorediate *P. crocata* also exhibits a variety of ecotypic forms; in fact morphological diversity in this taxon is somewhat greater than that seen in *P. intricata*. Accessory depsides and depsidones occur in *P. intricata* (Galloway & James, 1986), although stictic, salazinic, and consalazinic acids which are recorded from Indian Ocean collections are not found in specimens from New Zealand. Variation in *P. intricata* is also discussed by Coppins & James (1979) and by Galloway & James (1980).

Pseudocyphellaria intricata is distinguished from the related species *P. argyracea* which has delicate, simple to coralloid isidia at the lobe margins and also at the margins of laminal pseudocyphellae which do not form soredia. In a number of cases pseudoisidia are formed at the margins of laminal soralia and are then difficult to separate from forms of *P. argyracea* where the laminal isidia may lose their cortex and become ± sorediate. It is possible that a continuum of forms exist between strictly sorediate *P. intricata* and strictly isidiate, laminally pseudocyphellate *P. argyracea*. Detailed field work should elucidate this point. *P. intricata* is distinct from the sorediate *P. haywardiorum* (from northern New Zealand and north eastern Australia) which has a strongly punctate-impressed upper surface and a dark red-brown, bullate lower surface, and prominent numerous white pseudocyphellae.

Distribution: (Fig. 83) Throughout both main islands from Radar Bush, North Auckland (lat. 34°25′S), to Invercargill, and on Stewart I., from Oban to Port Pegasus, sea-level to 1150 m.

Habitat ecology: *Pseudocyphellaria intricata* is primarily a forest species, growing on bark, amongst other lichens, and in very damp, humid, shaded habitats amongst mosses on twigs of shrubs. It is tolerant of a wide range of light regimes, being found in dense shade, and from rocks exposed to full sunlight at forest and scrub margins in areas of moderate to high rainfall. Generally, it is a good indicator of moist, humid habitats and associates with the following lichens: *Coccocarpia palmicola*, *Coenogonium implexum*, *Collema* spp., *Degelia gayana*, *Hypotrachyna sinuosa*, *Hypogymnia subphysodes*, *Heterodermia podocarpa*, *Leioderma amphibolum*, *L. pycnophorum*, *L. sorediatum*, *Leptogium brebissonii*, *Nephroma rufum*, *N. cellulosum*, *Normandina pulchella*, *Pseudocyphellaria argyracea*, *P. crocata*, *P. bartlettii*, *P. fimbriatoides*, *P. glabra*, *P. hookeri*, *Psoroma leprolomum*, *P. sphinctrinum*, *Sticta fuliginosa*, *S. limbata*, *S. martinii*, *S. subcaperata*, *Usnea arida*, and *U. torquescens*.

It is an epiphyte of the following phorophytes: *Beilschmiedia tawa*, *Carpodetus serratus*,

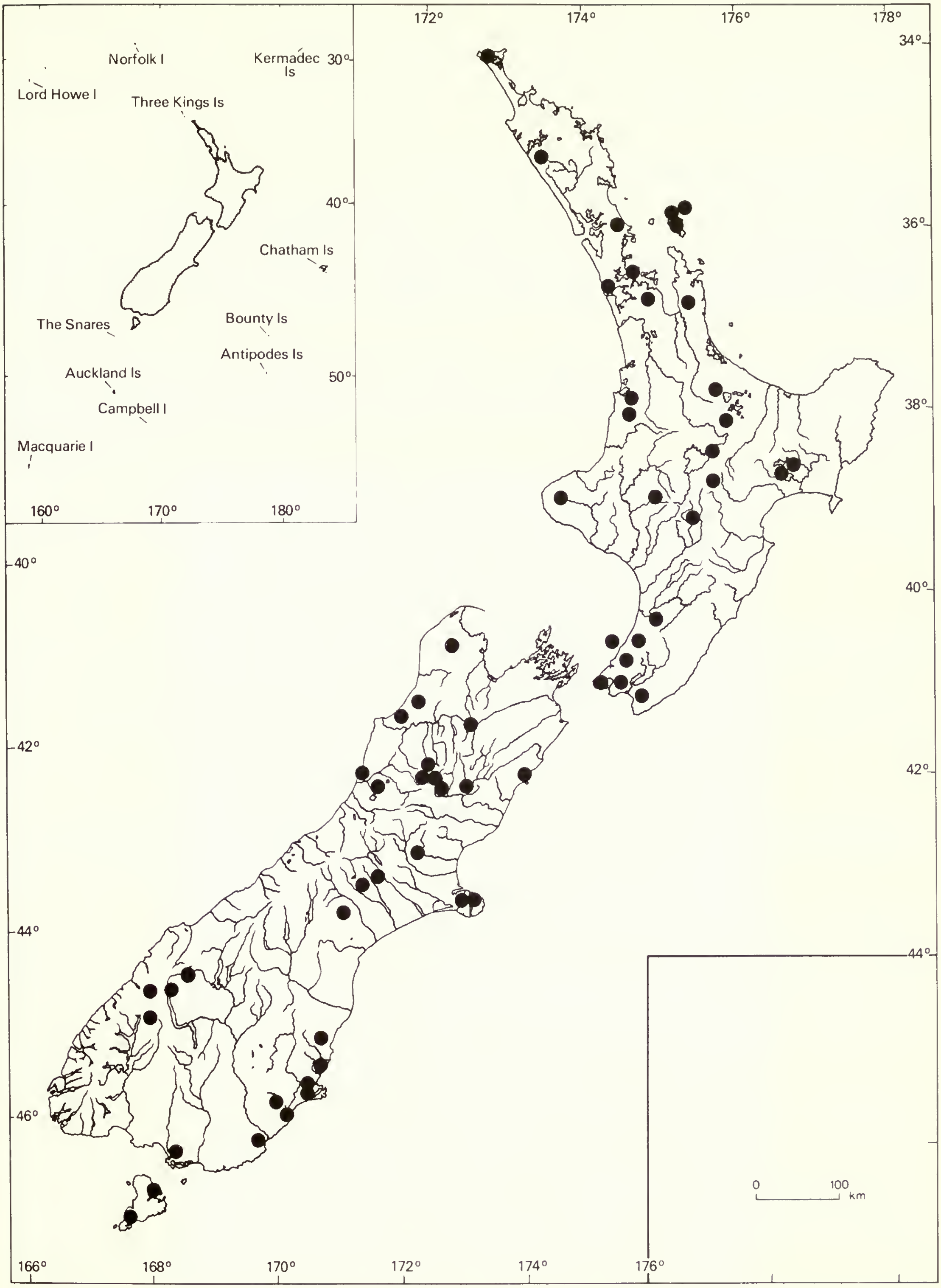

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Fig. 83 Distribution of *Pseudocyphellaria intricata*.

Dacrycarpus dacrydioides, *Dodonaea viscosa*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *Myrtus bullata*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Pennantia corymbosa*, *Rhopalostylis sapida*, and *Weinmannia racemosa*.

Specimens examined: 106.

30. **Pseudocyphellaria jamesii** D. Galloway, **sp. nov.** **Fig 84**

Diagnosis: Pseudocyphellariae coerulescentis similis sed lobis parvis, angustis, pagina superior passim tomentosus, subtus luteolus, pseudocyphelliis sparsis, minutis, immarginatis. Apothecia ignota. Typus: New Zealand, South I., Canterbury, Boyle River near Lewis Pass, on twigs of *Leptospermum scoparium* on terraces behind Boyle Lodge growing with *P. maculata*, September 1981. *P. W. James* (BM! – holotype). [t.l.c.: pulvinic acid, pulvinic dilactone, calycin, and a mixture of stictane triterpenoids similar to those found in *P. ardesiaca*.]

Morphology: *Thallus* rosette-forming, 2–5(–8) cm diam., loosely attached centrally, ± free at margins, corticolous. *Lobes* rather short and narrow, 1–2 mm, rarely to 8–10 mm wide, 0·5–2·5 cm long, concave to plane or shallowly convex, subdichotomously branching and ± discrete at margins to ± rounded, imbricate-folded marginally, complexly folded, imbricate centrally.

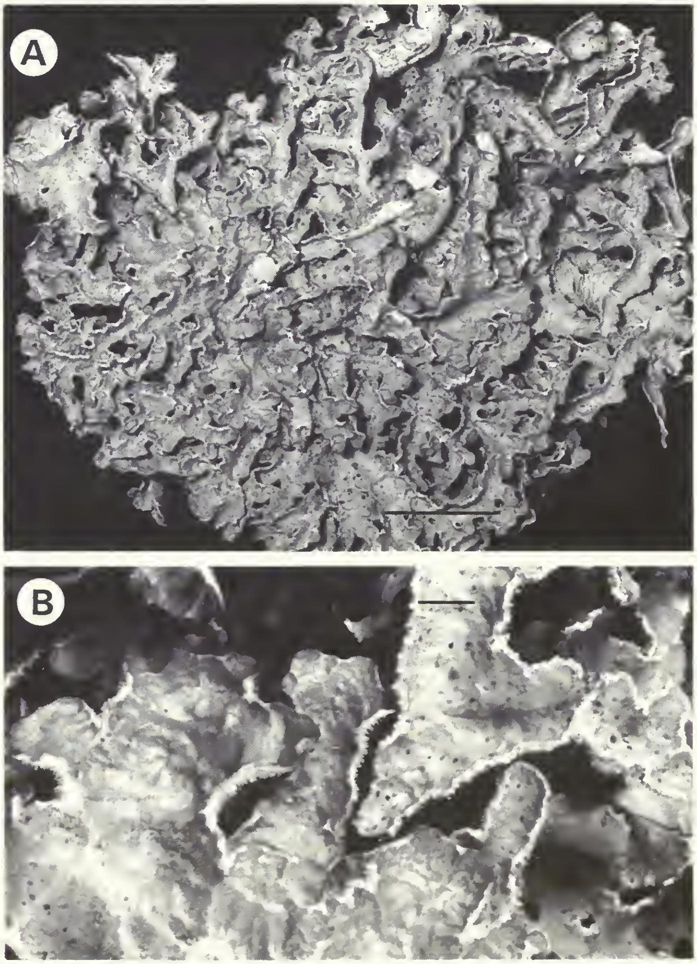

Fig. 84 *Pseudocyphellaria jamesii*. Boyle River, *Galloway* (CHR 374943). Scale = 1 cm. B. Scale = 1 mm.

Margins slightly thickened below, slightly ascending, sinuous above, rarely entire, more usually crenate, notched or occasionally minutely lobulate, with conspicuous, raised verruciform, yellow pseudocyphellae. *Upper surface* dark grey-blue suffused red-brown at apices when moist, pale grey-blue or glaucous-blue when dry, cyanobiont-free areas yellow-buff, shallowly to strongly reticulate faveolate at margins, ridges less obvious centrally, or ± irregularly wrinkled-plicate, here and there patchily tomentose, tomentum thin, pale buff to ± whitish, marginal and laminal, matt, without soredia, isidia, phyllidia or pseudocyphellae. *Maculae* prominent, yellow or whitish, laminal and marginal, effigurate to ± reticulate, most obvious when moist. *Medulla* yellow. *Photobiont Nostoc. Lower surface* pale yellow to ± buff, distinctly wrinkled or irregularly ridged, papillate or ± bullate, tomentose from margins to centre, tomentum thin to thick, white, silky, woolly entangled. *Pseudocyphellae* rather sparse, scattered, minute 0·1 mm diam. or less, on raised conical verrucae, decorticate area flat, immarginate, ± sunk in tomentum. *Pycnidia* scattered, laminal, rather sparse, 0·05–0·15 mm diam., slightly papillate, ostiole dark red-brown to black, punctate-depressed. *Apothecia* not seen.

Anatomy: Thallus 135–185(230–310) µm thick. *Upper cortex* 25–30 µm thick, upper 10–12 µm pale straw-yellow to yellow-brown, cells compressed, remainder colourless, cells 2·5–9 µm diam. *Tomental hairs* occasional, colourless, to 7 µm diam. and to 50 µm long. *Photobiont layer* 36–90(–130) µm thick, *photobiont Nostoc*, cells 4·5–7 µm diam. *Medulla* 34–140 µm thick, hyphae to 4·5 µm diam., thickly encrusted with yellow crystals. *Lower cortex* 13·5–22 µm thick, colourless to pale straw-yellow, cells 4·5–9 µm diam. *Tomental hairs* colourless, septate, locules short, constricted at septa appearing moniliform, 4–6 µm diam., 45–140(–185) µm long, singly or in fascicles.

Chemistry: As above.

Pseudocyphellaria jamesii is named in honour of Peter W. James (BM) in recognition of his collections of, and researches into Southern Hemisphere lichens; most notably of the chemistry and taxonomy of *Menegazzia*, *Nephroma*, and *Pseudocyphellaria.* He has made fine collections of *Pseudocyphellaria* from New Zealand, Tasmania, and Patagonia and in 1962–63, while on leave in Dunedin, New Zealand, he discovered photosymbiodemes of *Dendriscocaulon* and *Sticta filix* at Lake Thompson in Fiordland National Park, a discovery which led to a later important monograph (James & Henssen, 1976) on lichen cephalodia.

Distinguishing features: Pseudocyphellaria jamesii is a small, australasian, rosette-forming species characterized by a yellow medulla and blue-green photobiont, and a ± maculate upper surface lacking either soredia or phyllidia. It is not known fertile and it has a chemistry similar to that of *P. ardesiaca* and *P. nermula.*

Variation: P. jamesii is a species of ± constant morphology, showing only a slight variation in the width of lobes and also some variation in the extent and density of tomentum (Fig. 84B) on the upper surface (from completely glabrous to tomentum scattered in ragged patches). Marginal lobules are sometimes developed but their appearance is rare and spasmodic and it is not known what ecological conditions influence their formation. *P. jamesii* is distinguished from two related yellow-medulla species with which it is sometimes sympatric; from *P. ardesiaca* in lacking soredia and from *P. nermula* in lacking phyllidia.

In several earlier accounts (Galloway & James, 1980; Arvidsson & Galloway, 1981; Galloway *et al.*, 1983*b*; Galloway, 1985*b*) *P. jamesii* was recorded as *P. coerulescens*, a vicariant South American species not known from New Zealand. *P. coerulescens* differs from *P. jamesii* in several respects: its lobes are wider and longer (0·5–1·5 cm × 5–10(–15) cm), plane or convex and not so strongly faveolate; the upper surface is smooth, shining, here and there minutely papillate but not tomentose (use × 10 lens); the lower surface is pale yellow and glabrous at margins, dark grey to blackened tomentose centrally; and the pseudocyphellae are larger (0·1–0·8 mm diam.) with conspicuous, raised margins.

Distribution: (Fig. 85) *Pseudocyphellaria jamesii* is a rare and local species known only from montane to subalpine habitats in South I., east of the Main Divide from Nelson (near Lake

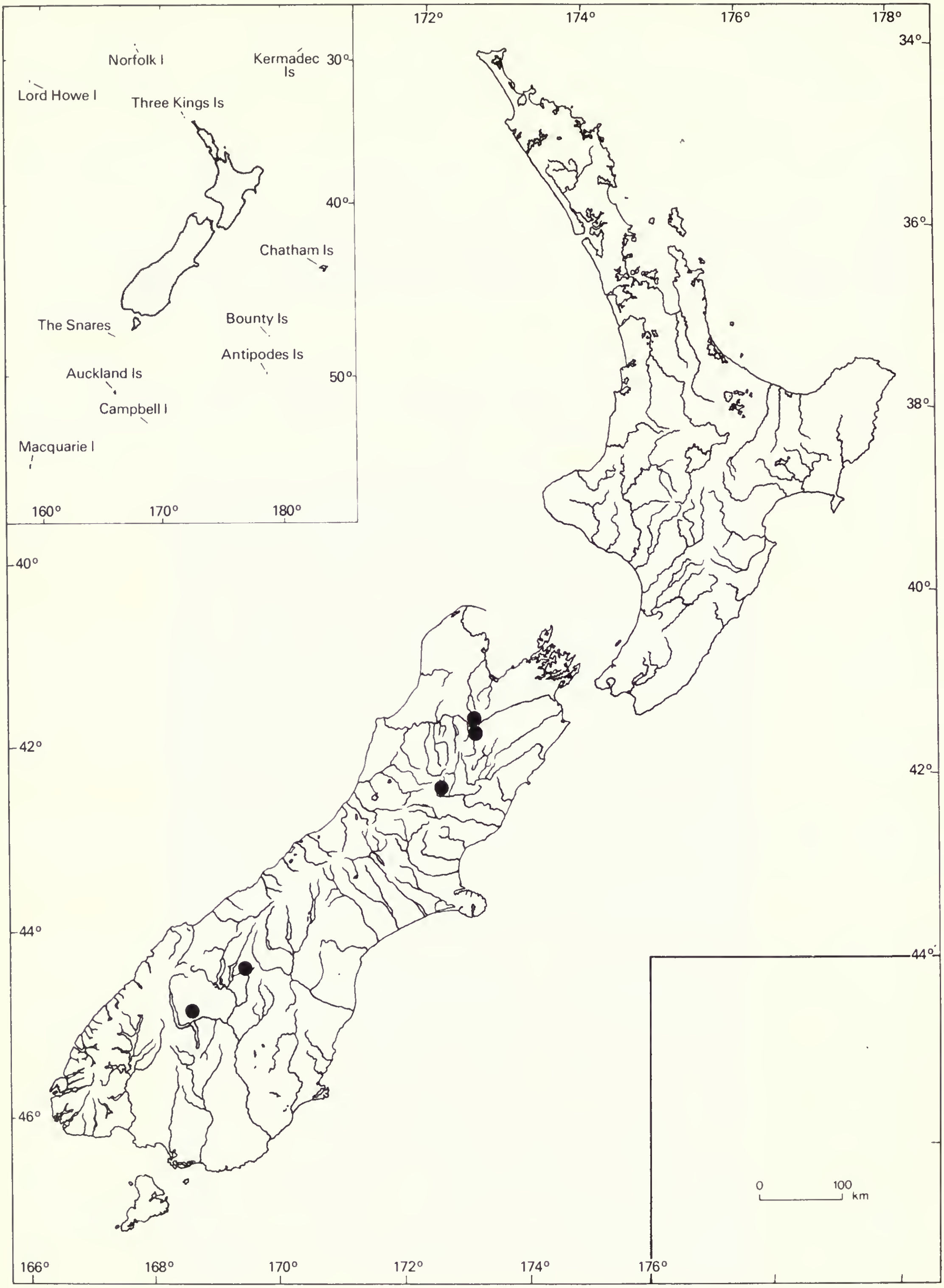
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Fig. 85 Distribution of *Pseudocyphellaria jamesii*.

Rotoiti) to Central Otago, 200–900 m. It also occurs in South-eastern Australia where it appears to be rare.

Habitat ecology: *Pseudocyphellaria jamesii* occurs in successional habitats altered by fire in the northern part of its range, on twigs and/or bark of *Leptospermum* in river flats, terraces, and on the shores of Lake Rotoiti. In Central Otago it is found on soil overlying schist rock in much drier, open, *Leptospermum*-shrubland habitats. In more humid habitats it associates with the following lichens: *Anzia jamesii*, *Coccocarpia erythroxyli*, *C. palmicola*, *Degelia duplomarginata*, *Erioderma sorediatum*, *Hypogymnia lugubris*, *H. mundata*, *H. subphysodes*, *Lobaria scrobiculata*, *Leioderma amphibolum*, *L. pycnophorum*, *Menegazzia dielsii*, *M. pertransita*, *M. subpertusa*, *Normandina pulchella*, *Nephroma australe*, *N. cellulosum*, *N. rufum*, *Pannaria fulvescens*, *Pannoparmelia angustata*, *P. wilsonii*, *Pseudocyphellaria ardesiaca*, *P. coronata*, *P. crocata*, *P. dissimilis*, *P. faveolata*, *P. glabra*, *P. maculata*, *P. nermula*, *P. pickeringii*, *P. rubella*, *Psoroma euphyllum*, *P. durietzii*, *P. leprolomum*, *P. sphinctrinum*, *Sticta limbata*, *Usnea capillacea*, and *U. pusilla*.

Specimens examined: South Island. Nelson: Takaka Hill, *J. K. Bartlett* (Herb. Bartlett); St Arnaud, Lake Rotoiti, Black Hill, 19 November 1977, *D. J. Galloway* (CHR); West Bay, Lake Rotoiti, 15 November 1977, *D. J. Galloway* (CHR) Canterbury: Boyle River, 11 January 1979, *D. J. Galloway* (CHR); September 1981, *P. W. James* (BM); Otago: Tarras, 14 May 1978, *J. K. Bartlett* 30478 (Herb. Bartlett); Arrowtown, 3 September 1981, *J. K. Bartlett* (Herb. Bartlett).

31. Pseudocyphellaria knightii D. Galloway **Fig. 86**

in *Lichenologist* **15**: 143 (1983). Type: New Zealand, South I., Nelson, five miles north of Westport, on bark of *Dacrycarpus dacrydioides* on side of small stream, March 1980, *D. J. Galloway* (CHR 375745! – holotype, BM! – isotype).

Morphology: *Thallus* irregularly spreading, 3–10(–15) cm diam., uniformly closely attached or loosely attached centrally, marginal lobes free, flat or ± ascending, corticolous. *Lobes* linear-laciniate, 2–5(–12) mm wide, 10–30(–70) mm long, discrete from margins to centre, or more often ± imbricate-complex, apices rounded, truncate or shallowly notched or incised, ± canaliculate to flat. *Margins* entire to shallowly notched or incised, sinuous, often ± ascending and lobes appearing canaliculate, slightly thickened, and inrolled below, sometimes beset with short tufts of tomentum or with tomentum projecting from lower surface, rarely with scattered, white, punctiform pseudocyphellae. *Upper surface* dark grey-black or bluish black, suffused red-brown at apices when moist, pale greyish brown or fawn, suffused red-brown or cinnamon in parts when dry, undulate, smooth to minutely wrinkled, pitted or papillate, matt, somewhat coriaceous, without soredia, isidia or phyllidia. *Maculae* minute, white, effigurate, most noticeable at lobe margins (× 10 lens) but also giving lamina a mottled appearance when moist, larger areas of photobiont-free tissue often present as irregular, buff, pink or brown patches. *Pseudocyphellae* frequent, scattered, white, 0·1 mm diam. or less, rarely to 0·2 mm diam., fleck-like, decorticate area flat, shallowly punctiform to very slightly raised. *Medulla* white. *Photobiont Nostoc. Lower surface* pale buff to grey-brown, densely tomentose to margins, tomentum brown or brown-black or red-brown, densely entangled, woolly, often projecting beyond lobe margins. *Pseudocyphellae* rather sparse, often difficult to see in thick tomentum, rarely conspicuous, raised, to 0·5 mm diam. (normally 0·1 mm) occasionally with prominent, white decorticate area, more usually decorticate area flat, buff, brown or dirty white, very inconspicuous. *Pycnidia* scattered, marginal, submarginal to laminal, solitary to 3-4-together, hemispherical, 0·1–0·3(0·5) mm diam., ostiole red-brown to black, punctate-depressed. *Apothecia* very rare (only seen once), sessile, rounded 2–3 mm diam., plane to subconvex, or shallowly undulate, disc pale red-brown, matt, smooth, epruinose, exciple translucent when moist, pale flesh-coloured, restricted to a narrow, irregular margin, ± scabrid-areolate or roughened below disc.

Anatomy: *Thallus* 130–230(–280) μm thick. *Upper cortex* 40–45 μm thick, upper 10–12 μm straw-yellow, cells tightly compacted, to 4·5 μm diam., remainder colourless, to 9 μm diam.

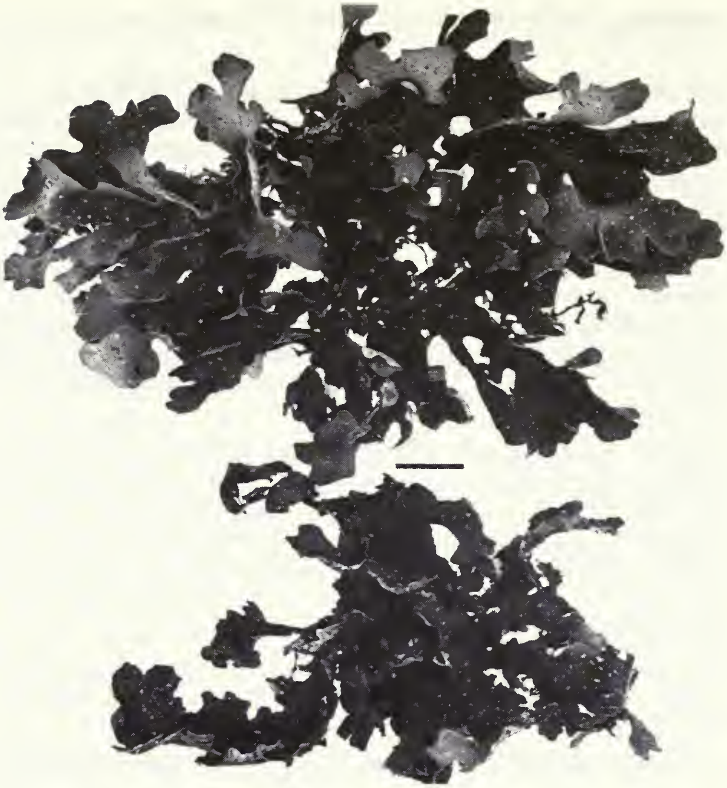


Fig. 86 *Pseudocyphellaria knightii*. Holotype (CHR). Scale = 1 cm.

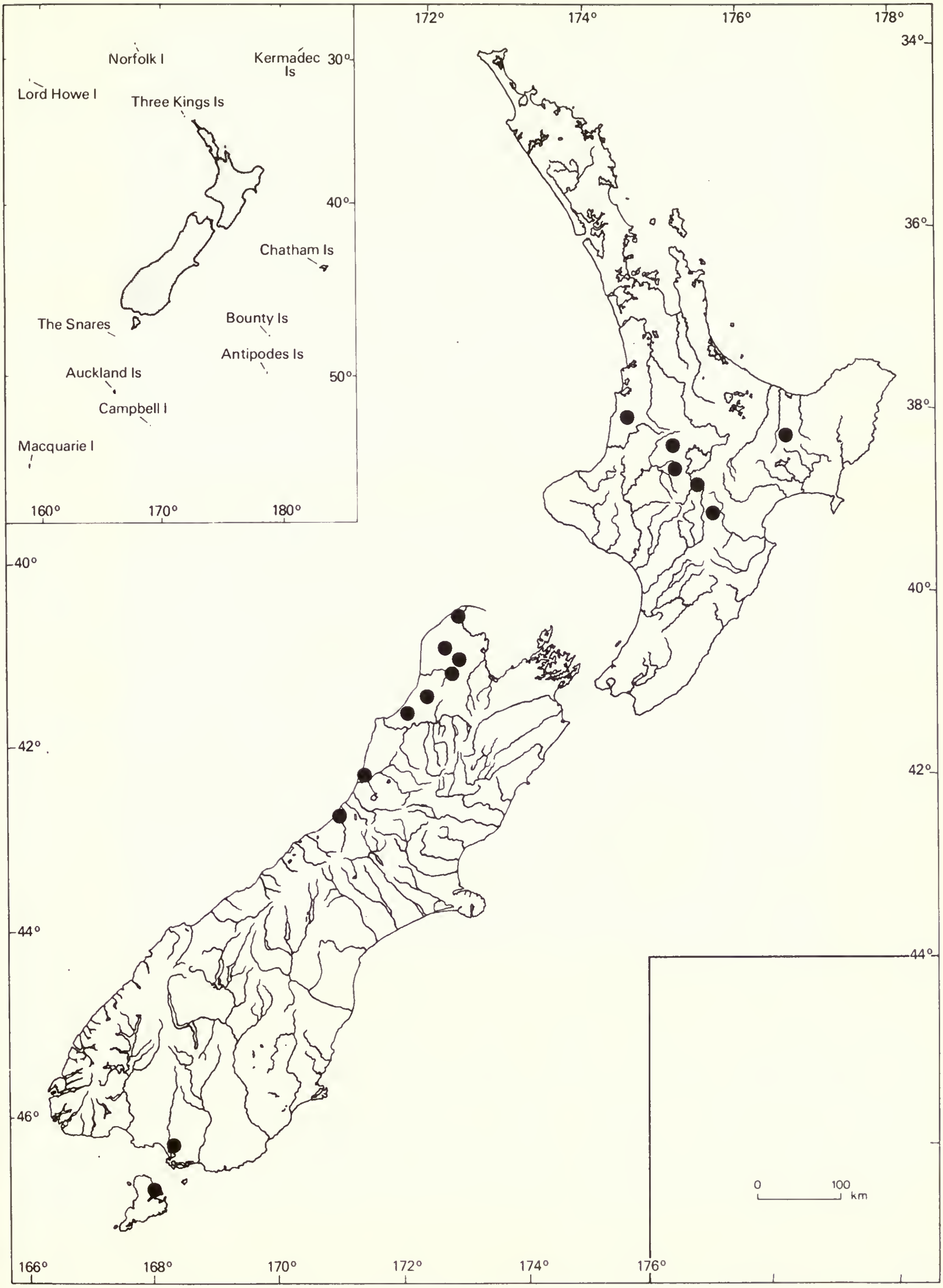
Photobiont layer 34–45 μm thick, photobiont *Nostoc*. *Medulla* 45–90(–180) μm thick. *Lower cortex* 27–32 μm thick, colourless, cells 6–13 μm diam. *Tomental hairs* colourless, 45–140 μm long, single or in sparse fascicles. *Apothecia: Exciple* colourless, 90–140 μm thick, poorly developed at margins of disc, cells 5–18 μm diam. *Hypothecium* pale straw-yellow unchanged in K, 46–75 μm thick. *Thecium* colourless, 90–100 μm tall: *epithecium* 11–15 μm thick, pale yellow-brown to red-brown, translucent, dissolving in K. *Asci* 58–82 × 13·5–15 μm. *Ascospores* pale yellow-brown to brown, fusiform-ellipsoid, apices pointed or one end rounded, 1-3-septate, (25–)27–32 × 9–11·5 μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Pseudocyphellaria knightii is named for Charles Knight (1808–1891), the distinguished 19th century New Zealand lichenologist whose herbarium contains many well-annotated and beautifully illustrated species of *Pseudocyphellaria*. He collected the genus widely, sending material of it to Kew, Paris, Geneva, Munich, and Vienna, with selected specimens distributed in the exsiccati of Arnold and of Lojka.

Distinguishing features: Pseudocyphellaria knightii is an endemic species having linear-laciniate to somewhat rounded-flabellate lobes, with entire to shallowly incised margins. The upper surface is undulate, coriaceous, smooth or slightly wrinkled, with minute, white maculae visible (× 10 lens) near margins, and with frequent, scattered, white pseudocyphellae. It has a white medulla, a blue-green photobiont, and a pale buff or grey-brown, thickly tomentose lower surface with rather sparse, white pseudocyphellae. It has a two-hopane chemistry [Code A of Wilkins & James (1979)], and is only very rarely fertile.

Variation: Pseudocyphellaria knightii is still a rather seldom collected species and such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Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
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Fig. 87 Distribution of *Pseudocyphellaria knightii*.

specimens as have been examined show a rather uniform morphology. It is related to *P. lividofusca* (both have the same chemistry and occasionally form photosymbiodemes) but it is distinct from it in having a blue-green photobiont and rather thinner, more fragile lobes. It is similar to a palaeotropical species *P. semilanata*, known from Fiji and Samoa, but this latter species has a punctate-impressed upper surface, narrower lobes, and it is besides often fertile. An Australian species, frequent in the rain forests of Queensland, *P. punctillaris*, is similar to *P. knightii* but has a thicker, more coriaceous thallus and has distinctly tomentose-pubescent lobe margins and apices.

Distribution: (Fig. 87) North I., from lat. 35°20′S, to West of Lake Taupo, and the Kaweka Range and in South I., from Nelson (Kaihoka Lakes) to Westland (Lake Mahinapua), also from the Waihopai Scenic Reserve (Invercargill), and from Stewart I., sea-level to 1410 m.

Habitat ecology: Pseudocyphellaria knightii is still very incompletely known. It is a species of moderate to deep shade, being found on logs on the forest floor, at the bases of forest trees, and on the bark and twigs of trees and and shrubs, and is known from the following phorophytes: *Agathis australis*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Dracophyllum traversii*, *Hoheria glabrata*, *Leptospermum scoparium*, and *Nothofagus solandri* var. *cliffortioides*.

Specimens examined: 16.

32. **Pseudocyphellaria lindsayi** D. Galloway, **sp. nov.** **Fig. 88**

Diagnosis: Pseudocyphellariae lividofuscae similis sed pagina inferior pallidus vel bubalinus, epithecio granulatus, K+ roseus, sporae 1-3-septatae, fuscae, 32–41 × 7–9 μm. Typus: New Zealand, South I., Nelson, Denniston Plateau north of Westport, on *Nothofagus menziesii* near road, 500 m, 21 September 1981, *D. J. Galloway* (BM! – holotype, CHR-isotype). [t.l.c.: 15α-22-dihydroxy-24-hopanoic acid, 15α-acetoxy-22-hydroxyhopan-24-oic acid (±)].

Morphology: Thallus orbicular to irregularly spreading, 5–12(–20) cm diam., closely attached centrally, margins ± free, often ascending, corticolous. *Lobes* ± linear-elongate or elongate-flabellate, apices rounded, discrete, occasionally contiguous to centre or more often complex-imbricate centrally, sinuses circular. *Margins* entire, sinuous, occasionally delicately and shallowly notched or incised, slightly thickened below. *Upper surface* bright lettuce-green, suffused brown or red-brown in parts and at margins, with occasional to frequent, minute, white to pale yellow-brown or red-brown papillae when moist, pale grey-green to pale fawn, suffused red-brown in parts when dry, undulate, plane or shallowly ridged or wrinkled, not faveolate, matt or shining, smooth, coriaceous, without soredia, isidia, maculae, or phyllidia. *Pseudocyphellae* occasional to frequent, white, conspicuous, 0·3 mm diam., generally much less, flat, fleck-like, shallowly to deeply punctate, ± verruciform, margins raised, prominent. *Medulla* white. *Photobiont* green. *Lower surface* smooth to wrinkled-plicate, tomentose from margins to centre or occasionally with a narrow, glabrous, marginal zone, tomentum pale whitish buff to chocolate brown centrally, thin, scattered, to thick woolly-entangled centrally. *Pseudocyphellae* numerous, prominent, small at margins, larger centrally, round to irregular, 0·05–1·2 mm diam., shallowly verruciform or papillate, margins distinct, concolorous with lower cortex, free of tomentum, decorticate area flat or convex or concave, white. *Pycnidia* sparse to frequent, often common in clustered groups at margins or scattered over lamina, 0·1 mm diam. or less, slightly raised, red-brown to black. *Apothecia* sessile, occasional to frequent, submarginal to laminal, rounded, 0·5–3 mm diam., concave at first then plane to shallowly convex, disc red-brown turning dark brown or black on drying, matt, epruinose, margins crenate-stellate or ± dentate, obscuring disc when young, exciple pale flesh-coloured or whitish, translucent when moist, conspicuously corrugate-scabrid.

Anatomy: Thallus 200–300 μm thick. *Upper cortex* pale straw-yellow to hyaline, cells 4–13·5 μm diam. *Photobiont layer* 35–55 μm thick, cells densely packed, *photobiont* green, cellular envelope prominent, 11 μm diam. *Medulla* 110–150 μm thick, colourless. *Lower cortex* 22–34

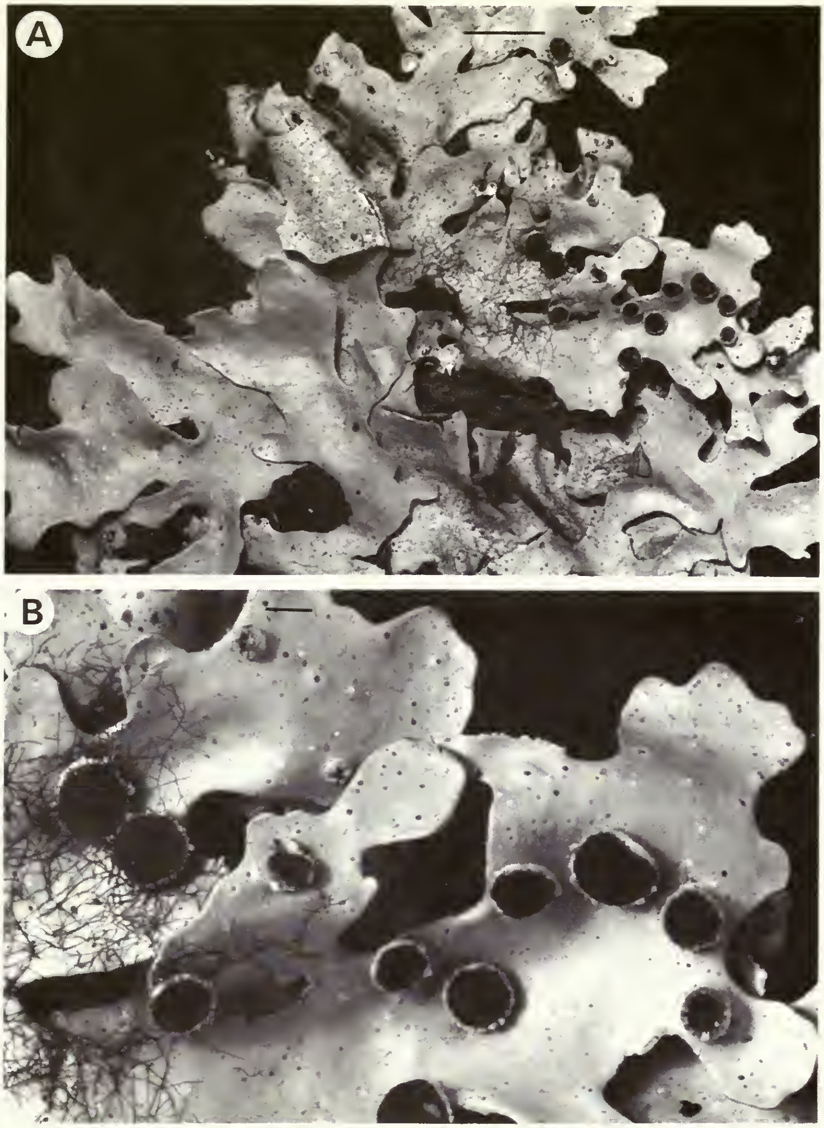

Fig. 88 *Pseudocyphellaria lindsayi*. Holotype (BM). A. Scale = 5 mm. B. Scale = 1 mm.

µm thick, colourless to pale straw-yellow, cells 4·5–12 µm diam., *tomental hairs* colourless, rather sparse, 45–150 µm long. *Apothecia: Exciple* colourless, 90–180(–230) µm thick, cells 7–15 µm diam. *Hypothecium* 45–60 µm thick, dilute red-brown or pale orange-brown, opaque. *Thecium* colourless, 80–105 µm tall; *epithecium* densely conglutinate, dark red-brown, densely granular, 11–22·5 µm thick, granules not dissolving in K, turning rose pink in K; *paraphyses* submoniliform at apices, granules external to tips. *Asci* 86–90 × 18–20 µm. *Ascospores* brown, fusiform, 1-3-septate, apices pointed, straight or curved, contents distinctly vacuolate, 32–41 × 7–9 µm.

Chemistry: as above.

Pseudocyphellaria lindsayi is named for the Scottish cryptogamist William Lauder Lindsay (1829–1880) who visited New Zealand in 1861 and who botanized extensively in the Otago Province. From these collections, both Lindsay and also William Nylander published several

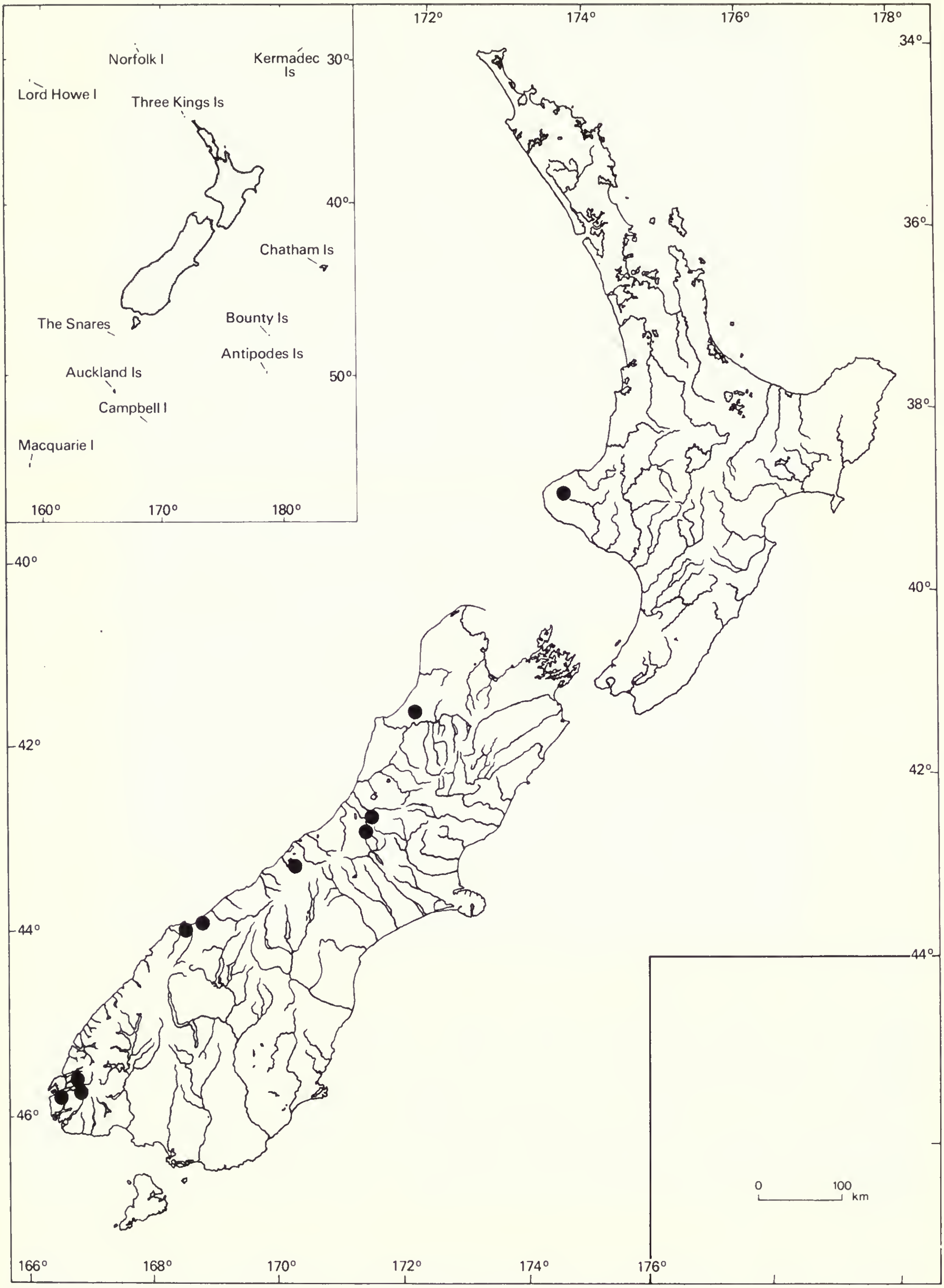
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Fig. 89 Distribution of *Pseudocyphellaria lindsayi*.

important papers, including many original observations on species of *Pseudocyphellaria*, then still included in *Sticta*.

Distinguishing features: *Pseudocyphellaria lindsayi* is an endemic species having linear-elongate or elongate-flabellate lobes, with entire, rounded margins, the upper surface has scattered, white pseudocyphellae, the medulla is white, the photobiont green, and the lower surface is pale whitish buff to brownish with numerous, white pseudocyphellae. Apothecia are submarginal to laminal, the disc red-brown to black and epruinose. Paraphyses are submoniliform at apices, the epithecium densely granular, the granules external to the paraphyses tips and dark red-brown, dissolving in K and turning rose-pink. The ascospores are fusiform, brown, 1-3-septate. The chemistry is characteristic containing 15α-acetoxy-22-hydroxyhopan-24-oic acid (±) and 15α-22-dihydroxy-24-hopanoic acid.

Variation: *Pseudocyphellaria lindsayi* is still a poorly collected species, the 10 specimens examined all having a similar and rather constant morphology. The species is closely similar to *P. lividofusca* and in several earlier accounts (Ronaldson & Wilkins, 1978; Galloway & James, 1980; Galloway *et al.*, 1983*b*; Galloway, 1985*a*) was included in the circumscription (as a chemodeme) of this latter species. However, it differs from it in several respects: the lower surface of *P. lindsayi* is pale whitish buff and not the ± uniform dark-brown of *P. lividofusca*, the epithecium is granular, red-brown, turning rose-pink in K (that of *P. lividofusca* is opaque, yellow-brown, and is unchanged in K), and the spores of *P. lindsayi* are longer (32–41 μm) than those of *P. lividofusca* (25–29·5 μm). The two species also each have a distinctive chemistry, with *P. lindsayi* containing hopane acids as primary constituents (amphistictinic acid of Ronaldson & Wilkins (1978)), whereas *P. lividofusca* has the normal two-hopane chemistry [Code A of Wilkins & James (1979)]. The entire, non-phyllidiate lobe margins distinguish *P. lindsayi* from *P. episticta* (the chemistry of the two species is the same).

Distribution: (Fig. 89) *Pseudocyphellaria lindsayi* appears to have a somewhat restricted distribution in New Zealand, being confined to high-rainfall areas west of the Main Divide in South I., from Nelson to Fiordland, and from Mt Egmont National Park, Taranaki in North I. It has an altitudinal range from sea-level to 990 m.

Habitat ecology: Little is known of the detailed habitat requirements, though it appears to favour high rainfall as evidenced by its collection from Westland and Fiordland rain-forest. It is an epiphyte of shrubs and trees being found amongst moss on bark in medium to low-light habitats, and associating with the following species of *Pseudocyphellaria: P. dissimilis*, *P. episticta*, *P. glabra*, *P. homoeophylla*, and *P. lividofusca*.

Specimens examined: North Island. Taranaki: North Egmont, along Veronica Walk, 26 November 1983, *L. Tibell* 15039 (UPS). South Island. Nelson: Denniston Plateau, 21 September 1981, *D. J. Galloway* (BM); sine loco (near Westport? Paparoa Range), *R. Helms* 90, 102 (W). Westland: Kelly's Hill, *W. Martin* (CHR); Otira, 17 September 1981, *H. J. M. Sipman* (BM). Southland: Mt Burnett, Dusky Sound, 15 February 1969, *R. M. Carter* (CHR); Oak Island, Wet Jacket Arm, Dusky Sound, 15 February 1969, *G. A. M. Scott* (CHR); Cook Stream, Pickersgill Harbour, Dusky Sound, 18 February 1969, *D. J. Galloway* (CHR).

33. **Pseudocyphellaria lividofusca** (Krempelh.) D. Galloway & P. James **Fig. 90**

in *Lichenologist* **12**: 300 (1980). – *Sticta lividofusca* Krempelh. in *Verh. zool.-bot. Ges. Wien* **26**: 448 (1876). Type: New Zealand, sine loco (prob. Wellington), *C. Knight* (M! – lectotype).

Sticta amphisticta Knight in *Trans. N.Z. Inst.* **12**: 267 (1888). Type: New Zealand, sine loco (prob. Wellington), *C. Knight* (WELT – Herb. Knight Vol. 16A p. 23! – lectotype; BM! WELT – Herb. Knight Vol. 36 p. 14! – isotypes). Fig. 90A

Morphology: *Thallus* orbicular to spreading, 5–10(–20) cm diam., loosely to closely attached centrally, margins free and ± ascending, corticolous. *Lobes* ± elongate-laciniate or flabellate, discrete from apices to centre, contiguous to ± imbricate, ± subdichotomously to complexly and irregularly branched, 0·4–1·5 cm wide, 1–5 cm long. *Margins* entire, rounded, shallowly

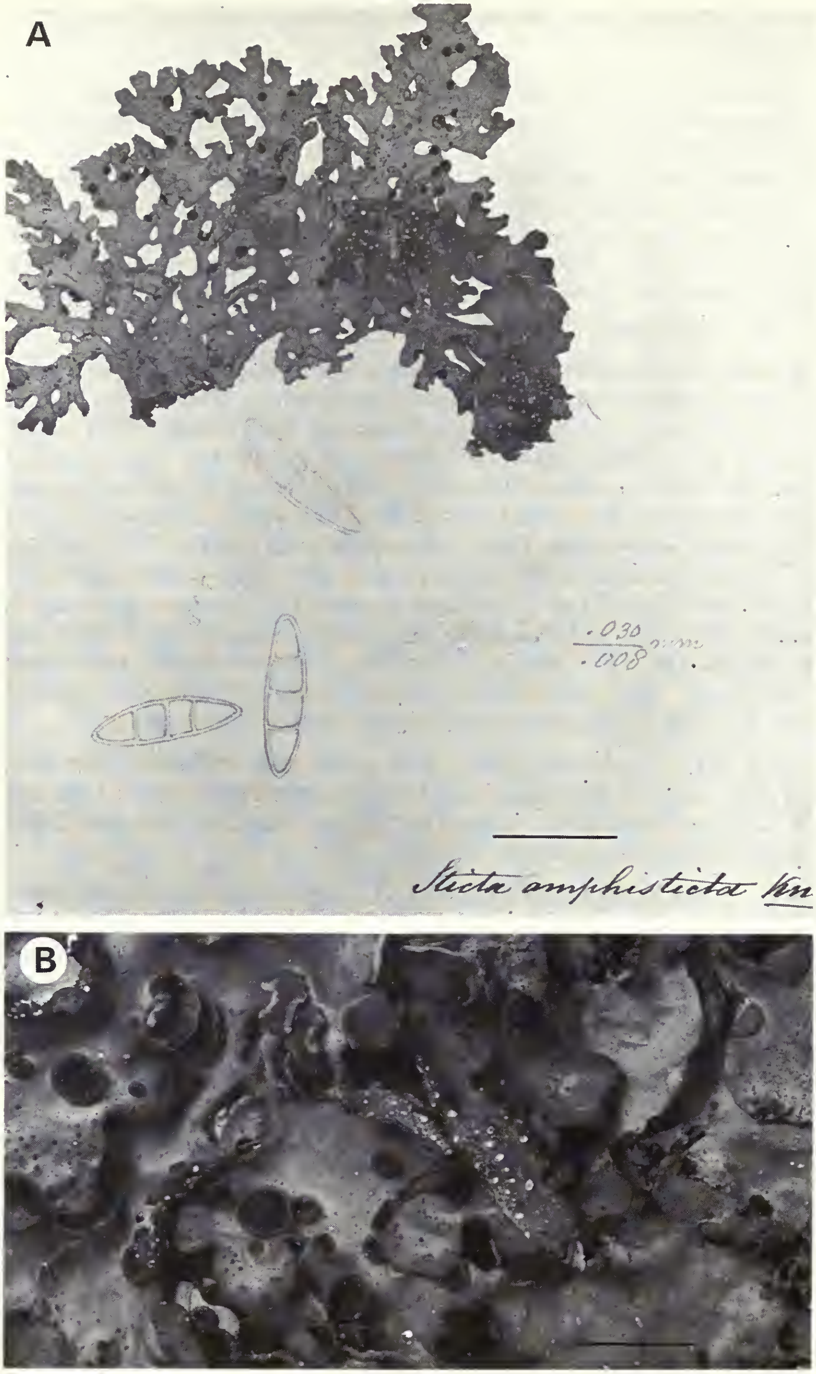


Fig. 90 *Pseudocyphellaria lividofusca*. A. Lectotype of *Sticta amphisticta* (WELT) Scale = 2 cm. B. *Helms* 28 (W). Scale = 5 mm.

scalloped, notched or incised, sinuous, subascendent in parts, markedly thickened or slightly ridged above and below, sinuses circular, prominent, often with brown tomentum projecting, without pseudocyphellae. *Upper surface* bright lettuce green to glaucous green suffused red-brown at apices when moist, pale greenish grey to brownish or red-brown when dry, plane or convex, shallowly and irregularly wrinkled or ridged, matt or shining, smooth, coriaceous, without soredia, isidia, phyllidia or maculae. *Pseudocyphellae* white, prominent, numerous, 0·1–1 mm diam., round to ellipsoid or ± linear, margins noticeably raised, decorticate area excavate, white. *Medulla* white. *Photobiont* green. *Lower surface* wrinkled or pitted, whitish or pale buff at margins, dark brown centrally, ± uniformly tomentose from margins to centre, or occasionally with glabrous patches at margins, tomentum thick, woolly, red-brown to dark brown or ± blackened, paler at margins. *Pseudocyphellae* common, prominent, round to irregular, 0·1–1·2 mm diam., ± conical verruciform, margins prominent, raised above tomentum or ± sunk in tomentum, decorticate area flat to excavate, white. *Pycnidia* common at or near margins, laminal, 0·1–0·3 mm diam., papillate or ± plane, ostiole prominent, dark red-brown to black. *Apothecia* occasional to frequent, scattered, submarginal and laminal, sessile to subpedicellate, round to irregular, 0·5–4 mm diam., shallowly concave to undulate-convex, disc pale to dark red-brown, smooth or minutely roughened, matt, epruinose, exciple whitish buff, translucent when moist, or pinkish to brownish, coarsely scabrid-verrucose, massive and obscuring disc as a verrucose plug at first, persisting as a verrucose-scabrid margin at maturity, often with coarse, pyramidal projections near disc.

Anatomy: *Thallus* 200–450 μm thick. *Upper cortex* 35–45 μm thick, uppermost 6–7 μm densely compressed, pale yellow-brown, cell structure not apparent, remainder colourless, cells 4·5–9 μm diam. *Photobiont layer* 22–35 μm thick, *photobiont* green, cells 7–9 μm diam., chloroplast filling cell. *Medulla* 110–300 μm thick, hyphae 2·5 μm diam. *Lower cortex* 22–35 μm thick, pale straw-yellow, cells 2–7 μm diam., *Tomental hairs* yellow-brown, to 5 μm thick, 50–210 μm long, in fascicles. *Apothecia: Exciple* colourless, 75–140 μm thick, yellow-brown at margins, cells 9–13·5 μm diam. *Hypothecium* pale straw-yellow, 55–75 μm thick, unchanged in K. *Thecium* colourless, 90–110 μm tall; *epithecium* 10–18 μm thick, yellow-brown, not granular, unchanged in K; *paraphyses* submoniliform, yellow-brown at apices. *Asci* (60–)76–82 × 18 μm. *Ascospores* pale brown or yellow-brown, 1-3-septate, ellipsoid with pointed or rounded ends, straight or curved, 24–29·5 × 7–9 μm.

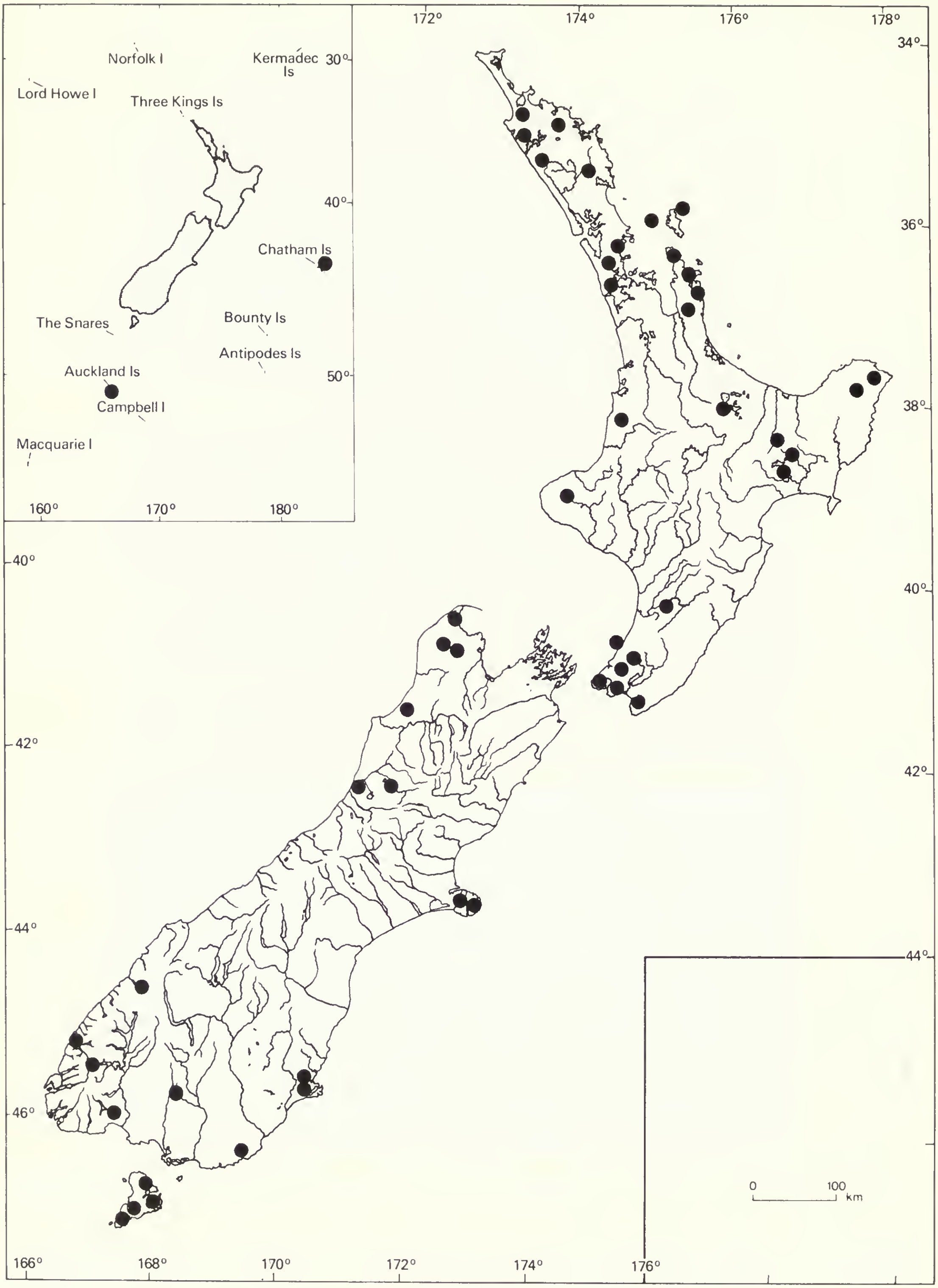
Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), and hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria lividofusca* is an endemic species characterized by broadly rounded, entire-margined lobes, with a smooth, coriaceous upper surface and prominent, scattered, white pseudocyphellae (Fig. 90B). It has a white medulla and a green photobiont. The lower surface is ± densely tomentose, ochraceous-brown to brown-black. Pseudocyphellae are white, numerous, with a ± prominent margin. Apothecia are submarginal, the disc red-brown; epithecium opaque, yellow-brown, unchanged in K, the spores are 1-3-septate, brown. It has a two-hopane chemistry [Code A of Wilkins & James (1979)].

Variation: This species shows rather little morphological variation apart from the dimensions of individiual thalli. When optimally developed it forms ± closely attached rosettes on bark and the colour of the upper surface may be suffused red-brown to a lesser or greater degree, depending on exposure to high light intensities. Individuals in high light habitats are noticeably livid red-brown in colour and have lobes more coriaceous and somewhat thicker than lobes from shaded habitats. It is distinguished from the closely related *P. lindsayi* (see above) by the colour of the lower surface, the shorter spores, the opaque epithecium (unchanged in K), and the different chemistry. The entire, non-isidiate, non-phyllidiate lobe margins separate it from *P. wilkinsii* which otherwise has similar spores, chemistry, and epithecium reaction in K.

Pseudocyphellaria lividofusca is distinguished from the superficially similar *Sticta subcaperata* by the scattered, white pseudocyphellae on both upper and lower surfaces (*S. subcaperata* has true cyphellae below) and the colour of the apothecia (yellow-orange in *S. subcaperata*). In addition, the two taxa are chemically distinct, with *S. subcaperata* lacking any triterpenoids or other acetone-soluble metabolites detectable by t.l.c.

Distribution: (Fig. 91) From North Auckland (lat. 35°S) to Wellington in North I., and in



Norfolk I
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Fig. 91 Distribution of *Pseudocyphellaria lividofusca*.

South I., from Nelson to Fiordland both east and west of the Main Divide. Also on Chatham I., Stewart I., and the Auckland Is. Coastal and inland, in montane to subalpine habitats, sea-level to 1000 m.

Habitat ecology: *Pseudocyphellaria lividofusca* is an epiphyte of coastal trees and sbrubs and also occurs inland in lowland forest and subalpine scrub. It prefers cool, moist, humid conditions, either alongside streams or riverbeds, or in areas where cloud cover is frequent and rainfall moderate to high, and where there is sufficient light. Individuals exposed to full sun have thicker, more coriaceous thalli suffused red-brown, whereas those from shaded habitats are thinner and ± pale green. Photosymbiodemes with *P. knightii* are known from forest habitats in Gisborne, North I., though they seem to be rare and local. *P. lividofusca* is most commonly a bark species, though small individuals are also found on twigs of shrubs in humid habitats associated with species of *Erioderma*, *Leioderma*, *Psoroma*, and *Pseudocyphellaria*. Elsewhere in its range it is often a prominent epiphyte on the boles of forest trees in association with *Brigantiaea chrysosticta*, *Coccotrema cucurbitula*, *Polychidium contortum*, *Lobaria adscripta*, *L. asperula*, *Hypogymnia subphysodes*, *Leptogium cyanescens*, *Parmelia tenuirima*, *Sticta filix*, *S. latifrons*, and numerous species of *Menegazzia*, *Pseudocyphellaria*, and *Psoroma*.

It is known from the following phorophytes: *Beilschmiedia tawa*, *Coprosma polymorpha*, *Cordyline australis*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Elaeocarpus dentatus*, *Griselinia littoralis*, *Knightia excelsa*, *Kunzea ericoides*, *Metrosideros lucida*, *Myrtus bullata*, *Nothofagus menziesii*, *N. truncata*, *Pittosporum*, *Podocarpus hallii*, *Quintinia serrata*, *Weinmannia racemosa*, and *W. silvicola*. *Pseudocyphellaria lividofusca* is also known from damp limestone on Mt Hoary Head (Nelson) and from coastal rocks on Ulva Island, Stewart I.

Specimens examined: 90.

Exsiccati seen: Ljoka. *Lich. Univ. III* (1886) 115 [as *Sticta amphisticta* Knight] BM! G! M! S! UPS! Ljoka: *Lich. Univ. III* (1886) 116 [as *Sticta sinuosa*] G!

34. **Pseudocyphellaria maculata** D. Galloway **Fig. 92**

in *Lichenologist* **15**: 143 (1983). Type: New Zealand, South I., Nelson, Maruia River, Speargrass Flat, near Springs Junction, on twigs of wayside shrubs, 22 September 1981, *D. J. Galloway* (CHR 381022! – holotype; BM! – isotype) [see also Galloway (1986*b*)].

Morphology: *Thallus* spreading in irregular rosettes or in ± erect clumps, (2–)5–10(–15) cm diam., loosely attached centrally when corticolous, straggling to ± erect when terricolous. *Lobes* laciniate-elongate, branching ± dichotomous at apices, more irregular to complex-imbricate in older parts, subcanaliculate to plane, 1–10 mm wide, 0·5–3(–5) cm long. *Margins* entire, slightly thickened, raised, dotted with minute, punctiform-eroded, yellow pseudocyphellae, apices irregularly shallowly dentate, furcate or blunt. *Upper surface* dark grey-blue, reddish brown at apices when wet and distinctly white-maculate in well-defined patterns (× 10 lens), pale greyish or greenish grey to greyish buff, reddish brown to cinnamon-brown centrally when dry, paler and greyer in shaded sites, suffused red-brown in exposed sites; shallowly to deeply faveolate, ridges between faveolae sharp and well-defined or smoothly rounded, faveolae deeply lacunose; matt or slightly nitid, often irregularly cracked, minutely scabrid-areolate in parts, slightly glossy at apices, without isidia, phyllidia, pseudocyphellae or soredia. *Medulla* white. *Photobiont Nostoc*. *Lower surface* distinctly wrinkled-bullate, pale yellowish buff or whitish at margins, buff-brown to dark red-brown centrally, ± uniformly tomentose from margins to centre, tomentum thin, silky, short, white or buff, becoming thicker and darker to red-brown centrally. *Pseudocyphellae* yellow, shallowly verruciform, minute, 0·1–0·3 mm diam., scattered, rather widely spaced, decorticate area ± convex, raised above or sunk in tomentum, margins not prominent. *Apothecia* marginal and laminal, occasional to moderately common in forest or scrub populations, very rare in alpine grassland populations, 1·5–3 mm diam., undulate, shallowly concave at first, plane to convex at maturity, subpedicellate, constricted at base, disc matt, epruinose, imperforate, pale to dark red-brown when wet,

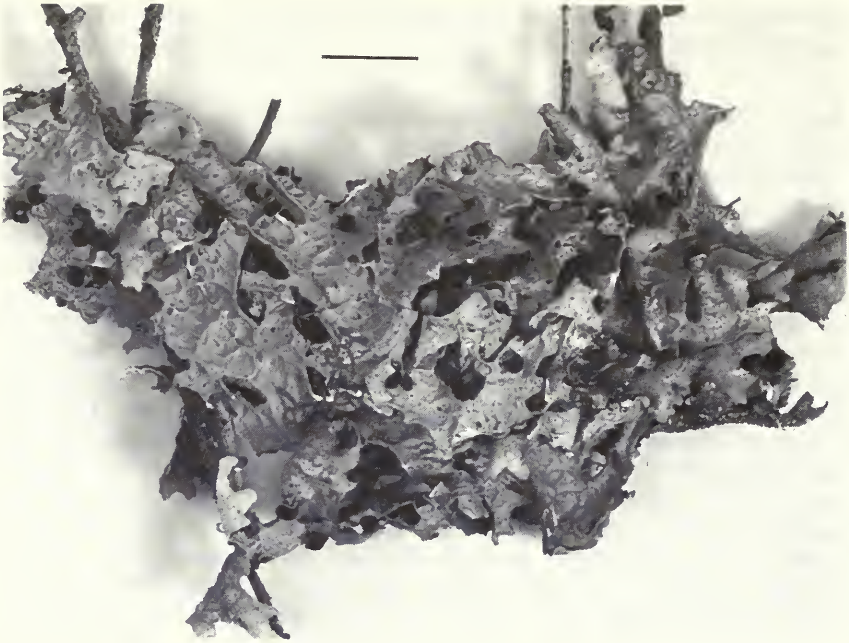

Fig. 92 *Pseudocyphellaria maculata*. Holotype (CHR). Scale = 1 cm.

brown-black when dry, exciple pale flesh-pink, coarsely scabrid-areolate and ± minutely tomentose-pubescent, wrinkled-faveolate near margins and projecting beyond disc in ± ragged clumps, persistent in mature fruits.

Anatomy: *Thallus* (130–)155–220(–275) μm thick. *Upper cortex* 20–20(–34) μm thick, uppermost 4–7 μm colourless (in forest forms) to red-brown (in grassland populations), with cells necrotic or stretched-compressed, internal 3–4 rows of cells colourless, cells 3–8 μm diam. *Photobiont layer* 45–65 μm thick, *photobiont Nostoc. Medulla* (45–)70–100(–130) μm thick, hyphae to 4 μm diam., encrusted with small crystals, pale yellowish-hyaline. *Lower cortex* 18–23 μm thick, lower 5–7 μm pigmented, pale yellow-brown, zone nearest medulla colourless. *Tomental hairs* simple, septate, 4–5 μm diam., colourless to yellow-brown, in fascicles of 6–12, 60–160 μm long. *Apothecia: Exciple* 60–85 μm thick, colourless, cells 7–14 μm diam., rows of cells projecting below main body of exciple as short, ragged tomentum, or in separated shallow pyramidal wedges of cells. *Hypothecium* 45–65 μm thick, dilute orange-brown. *Thecium* 65–75 μm tall, colourless; *epithecium* 6·5–11 μm thick, dark brown, minutely granular in grassland forms, pale yellow-brown in shade forms, becoming paler on addition of K. *Asci* 60–72(–80) × 18–20 μm. *Ascospores* brown, thickened, 1-septate, septum 3 μm thick, to 3-septate at maturity, over-mature spores sometimes spuriously 5-septate through disintegration of small apical locules, 23–25 × 7–9 μm.

Chemistry: Methyl evernate (tr.), tenuiorin, methyl lecanorate (tr.), methyl gyrophorate, evernic acid (tr.), gyrophoric acid (tr.), hopane-6α, 7β, 22-triol, norstictic (tr.), salazinic, consalazinic, galbinic acids, pulvinic dilactone, pulvinic acid, and calycin.

Distinguishing features: *Pseudocyphellaria maculata* has a white medulla, a blue-green photobiont, a conspicuously faveolate upper surface with a well-defined reticulate pattern of white (photobiont-free) maculae, best seen (× 10 lens) when thallus is wet, and yellow pseudocyphellae on the lower surface and visible at the lobe margins. It lacks isidia, soredia, phyllidia, pseudocyphellae, or tomentum on the upper surface. Its loose, straggling habit (especially in alpine grassland habitats where it is best developed) is also characteristic. It is rarely fertile, the spores brown, thickened, 1-3-septate. It has a characteristic and complex chemistry containing galbinic and salazinic acids, compounds rarely found in other species of *Pseudocyphellaria* in New Zealand.

Variation: Pseudocyphellaria maculata in alpine grassland habitats (Fig. 93) shows little morphological variation other than differences in size, texture, and colour, all dependent on local microclimate and microhabitat conditions. Individuals from moist, protected sites are larger, thinner in texture, and much less suffused red-brown than populations from exposed sites, which tend to be thicker, more mat-forming and darker coloured. In alpine populations the upper cortex is thicker (34 µm) than in populations from scrub and forest (20–27 µm), and the upper zone of the upper cortex is thicker (11 µm) and darker coloured (orange-brown) than it is in collections from sheltered and shaded sites. Similarly, the epithecium from alpine grassland collections is brown-black, while that from specimens in forest is dilute yellow-brown. Corticolous populations of *P. maculata* have broader, more spreading lobes, and are more commonly fertile than grassland forms (Fig. 92), but in all other respects (apart from those mentioned above) anatomical characters are entirely similar in both groups.

Pseudocyphellaria maculata is similar to *P. lechleri* (Müll. Arg.) Du Rietz, from South America, and in earlier accounts (Galloway & James, 1980; Galloway *et al.*, 1983*b*; Jørgensen & Galloway, 1983; Galloway, 1985*a*) the grassland populations were referred to this latter species. There are, however, good differences between the two vicariant taxa; *P. lechleri* has broader, more rounded lobes, forming neat rosettes on bryophytes, soil or decaying vegetation; it is more consistently fertile with the surface of its discs being granular to ± papillate; the epithecium is dark brown and granular; the thecium is suffused dark-brown; the hypothecium is dark red-brown, turning greenish-black in K, and the spores are slightly longer (22·5–)25–29·5 × 6·5–9 µm.

Pseudocyphellaria maculata is distinguished from *P. crocata* in lacking soredia, from *P. neglecta* in lacking phyllidia, and from *P. sericeofulva* in lacking smooth, ± cochleate lobes and laminal tomentum. *P. maculata* also differs from a group of faveolate taxa with green photobionts viz., *P. billardierei* which has a differing chemistry and white pseudocyphellae; *P. carpoloma* which has yellow pseudocyphellae but a distinctive chemistry containing several

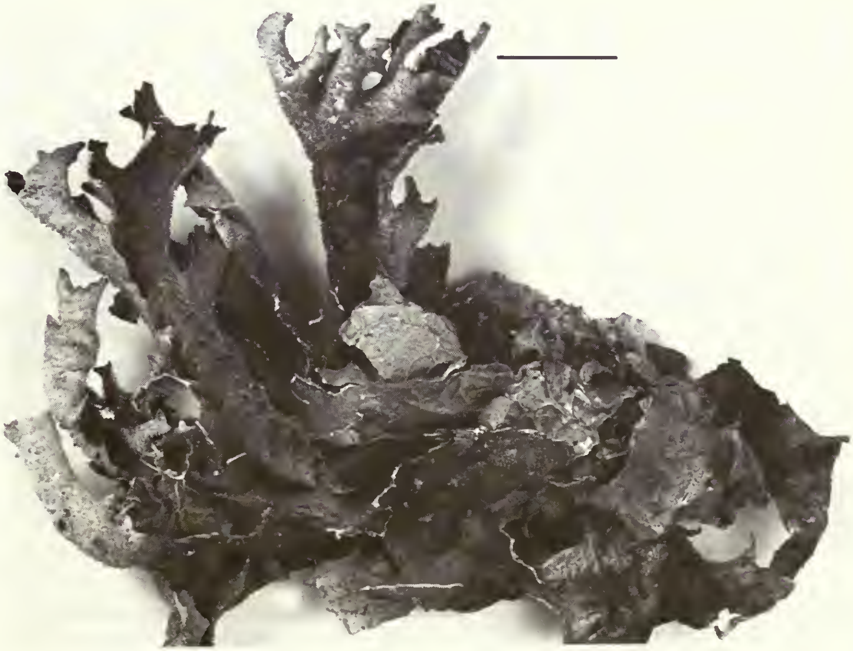

Fig. 93 *Pseudocyphellaria maculata*. Raglan Range, *Molloy* (CHR 375335). Scale = 1 cm.

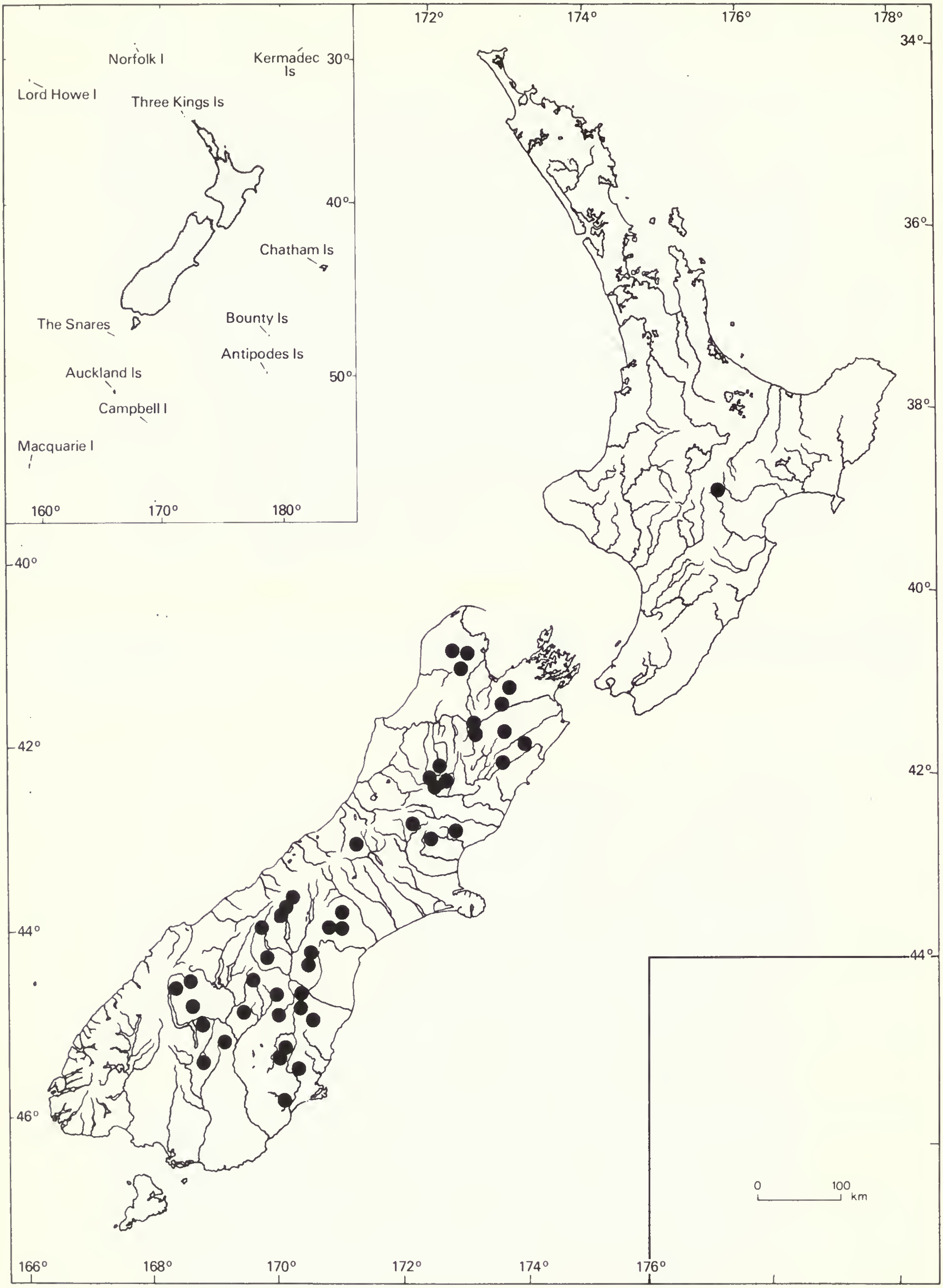
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Fig. 94 Distribution of *Pseudocyphellaria maculata.*

triterpenoids and compounds of the stictic acid aggregate but lacking galbinic and salazinic acid; *P. faveolata* which has white pseudocyphellae, white-pruinose apothecial discs, and a differing chemistry characterized by the depsidone physciosporin; and *P. physciospora* which has minute, yellow pseudocyphellae, entire margins without pseudocyphellae, and a chemistry that differs from that of *P. maculata* in having several triterpenoids, members of the stictic acid aggregate, and lacks galbinic acid; it also has somewhat broader lobes.

Distribution: (Fig. 94) North I., Hawkes Bay (Kuripapango), South I., north-west Nelson to Otago, close to and east of the Main Divide, in alpine grasslands or on successional shrubs in areas modified by fire, 300–2100 m.

Habitat ecology: Throughout its range in New Zealand, the endemic *P. maculata* is primarily a species of alpine to high-alpine grasslands dominated by species of snow tussock *Chionochloa* (*C. crassiuscula*, *C. pallens*, *C. rigida*). It prefers rather moist, shaded sites, flourishing at the bases of tussocks or beneath alpine shrubs and herbs including *Aciphylla* spp, *Cassinia fulvida*, *Celmisia viscosa*, *Dracophyllum longifolium*, *D. pronum*, *Gaultheria crassa*, and *Hebe* spp. In these sheltered habitats, thalli are larger and better developed, though thinner in texture and much paler in colour than individuals colonizing ± open ground among mosses on damp rock faces, on decaying cushion vegetation or in fellfield or scree exposed to the full rigours of a harsh alpine environment. Thalli from such exposed alpine sites are thicker and more coriaceous in texture and strongly red-brown in colour. Although mainly an alpine grassland species, *P. maculata* is also known from twigs and bark of *Leptospermum scoparium* and *Nothofagus solandri* var. *cliffortioides* in forest or scrub associations close to alpine grassland where fire has most commonly induced growth of successional vegetation. It seems to be a rather poor colonizer of corticolous habitats, unlike the grassland species *P. glabra* and *P. degelii* which grow with equal success in both grassland and forest. Above the Boyle River in north Canterbury close to the Lewis Pass, fire-induced grassland occurs as enclaves in the surrounding *Nothofagus* forest at altitudes below treeline, and in these grasslands *P. maculata* grows vigorously. However, it is absent from the surrounding forests both above and below the forest-enclosed grassland, and is found only occasionally on twigs of *Leptospermum* on terraces beside the Boyle River.

P. maculata associates with many subalpine to alpine lichens including *Alectoria nigricans*, *Arthrorhaphis alpina*, *Brigantiaea fuscolutea*, *Cetraria islandica* ssp. *antarctica*, *Hypogymnia lugubris*, *Lecanora broccha*, *Menegazzia aeneofusca*, *M. inflata*, *Parmelia signifera*, *Physma chilense*, *Pseudocyphellaria glabra*, *P. degelii*, *Psoroma buchananii*, *P. hirsutulum*, *Siphula decumbens*, *S. fragilis*, *Solorina crocea*, *Teloschistes fasciculatus*, *Thamnolia vermicularis*, *Toninia bullata*, and *Usnea contexta*.

Specimens examined: 48.

35. **Pseudocyphellaria margaretiae** D. Galloway **Fig. 95**

[*'margaretae'*] in *Mycotaxon* **16**: 203 (1982). Type: New Zealand, South I., Nelson, Nelson Lakes National Park, Lake Rotoiti, Peninsula, on *Kunzea ericoides*, 29 February 1980, *D. J. Galloway* (CHR 343279! – holotype, BM! – isotype).

Morphology: Thallus orbicular, rosette-forming to spreading, 5–8(–16) cm diam., loosely adnate centrally, margins ± free, corticolous. *Lobes* rather short, rounded, 2–10 mm diam., contiguous to complex-imbricate, convex to concave, undulate; margins entire, ± subascendent, sinuous, shallowly scalloped, slightly thickened below, occasionally with punctiform to short-linear, yellow pseudocyphellae, densely tomentose. *Upper surface* dark, livid, slate-blue suffused red-brown when wet, pale greyish pink or buff to ± red-brown when dry, ± densely and evenly tomentose from margins to centre, tomentum white, silky, entangled, minutely wrinkled-pitted to ± scabrid below tomentum, best seen when wet (× 10 lens), rarely ± glabrous and somewhat coriaceous in patches near centre, without isidia, pseudocyphellae or soredia. *Medulla* white. *Photobiont* blue-green. *Lower surface* pale yellow-buff at margins

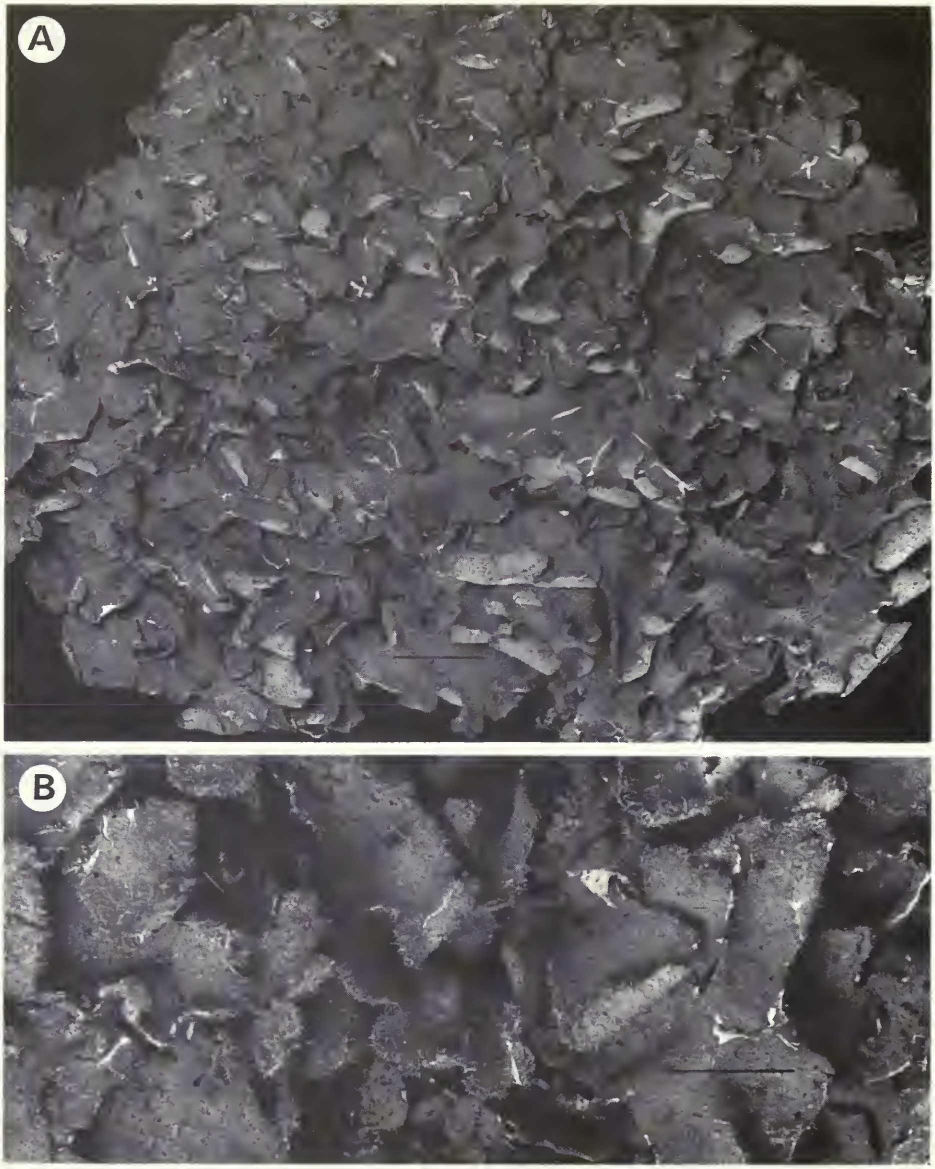

Fig. 95 *Pseudocyphellaria margaretiae*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 5 mm.

darkening centrally, densely tomentose to centre, tomentum white, silky, thick, long, often in dense fascicles (× 10 lens), occasionally long, tufted rhizines to 5 mm long in bundles anchor marginal lobes to substrate. *Pseudocyphellae* yellow, common, conspicuous, 0·1–1 mm diam., punctiform to ± linear, sunk in tomentum, ± flat or only very slightly raised from lower surface on shallow wrinkles, decorticate area flat. *Apothecia* not seen. Upper surface often parasitized by a lichenicolous fungus forming scattered, often dense clusters of small, black, shining conical fruits, 0·1 mm diam. or less.

Anatomy: *Thallus* 110–140(–180) μm thick. *Upper cortex* 27–36 μm thick, a pseudoparenchyma of 6–8 rows of anticlinally arranged, thick-walled, round to rectangular cells 4·5–11 μm diam., walls 2–2·5 μm thick, lumina round to rectangular, 2–7 μm diam., uppermost 10–12 μm dilute orange-brown, a layer of ± necrotic cells, zone adjoining photobiont layer colourless.

Photobiont layer 45–64 μm thick, *photobiont* blue-green, *Nostoc*, in round to irregular clusters, 22–45 μm diam., enclosed in a thin, gelatinous envelope, with loosely woven hyphae between. *Medulla* very variable in thickness, often rather thin, 30–45(–140) μm thick, very loosely interwoven of hyaline hyphae, ± periclinally arranged, to 4·5 μm diam., encrusted with small, granular crystals. *Lower cortex* very thin of 1–2 rows of thick-walled cells, 11–14 μm thick, pale yellow-brown to hyaline, cells similar in dimensions to those of upper cortex. *Tomental hairs* common, simple septate, colourless, 5 μm diam., slightly attenuating towards apices, in dense fascicles 45–90(–360) μm long, hairs of upper surface simple, very sparsely septate, singly or in fascicles 4–6(–10), 75–90(–140) μm long. *Spores* of lichenicolous fungus pale grey-brown, simple, oval-ellipsoid, 7–11·5 × 4·5 μm.

Chemistry: Methyl evernate (tr.), tenuiorin, methyl lecanorate (tr.), methyl gyrophorate, gyrophoric acid (tr.), hopane-15α, 22-diol, hopane-6α, 7β, 22-triol, norstictic (tr.), salazinic (tr.), stictic, cryptostictic (tr.), constictic (tr.) acids, pulvinic dilactone, pulvinic acid, and calycin.

Pseudocyphellaria margaretiae is named for Mrs Margaret Bulfin (née Simpson) formerly of Botany Division, D.S.I.R., Christchurch, New Zealand, who has studied for many years the vegetation and flora of the Nelson Lakes National Park where the lichen is most commonly collected.

Distinguishing features: *Pseudocyphellaria margaretiae* is a rosette-forming, endemic species having rather short, rounded, imbricate lobes with entire, densely and evenly tomentose margins without isidia, phyllidia, or soredia. It has a white medulla, a blue-green photobiont, and a pale-buff, densely tomentose lower surface with conspicuous yellow pseudocyphellae. It is not known fertile. It has a complex chemistry of pigments, hopane triterpenoids, depsidones, and metabolites of the stictic acid complex (Galloway *et al.*, 1983*b*; Galloway, 1985*a*).

Variation: *Pseudocyphellaria margaretiae* shows little morphological variation throughout its known range, and although often reaching a considerable size in the habitats in which it grows, it is not a common lichen. It is related to *P. pubescens*. The two species have a closely similar chemistry and occasionally form photosymbiodemes (Renner & Galloway, 1982), however, *P. margaretiae* differs from *P. pubescens* in the following respects: the lobes are shorter and more rounded-imbricate, the upper surface is not visibly faveolate or even markedly ridged, the surface of the lobes is uniformly tomentose, and the colour when moist is a livid grey-brown, because of the blue-green photobiont. By contrast, *P. pubescens* is green when moist, has longer and narrower lobes which are reticulate-faveolate, the upper surface is often glabrous, and the cortex ± distinctly roughened-scabrid. It is frequently fertile, and the marginal apothecia have black discs usually covered in a grey-white pruina. In some earlier accounts *P. margaretiae* was recorded as *P. hirsuta* (Martin, 1969*a*; Martin & Child, 1972; Galloway & Simpson, 1978); however, this distinctive South American taxon is not known from New Zealand. It differs from *P. margaretiae* in having much broader *Peltigera*-like lobes, conspicuous marginal, pedicellate apothecia with epruinose discs, and a different chemistry (Galloway, 1986*a*).

Distribution: (Fig. 96) Known from ± subalpine habitats mainly in north-west Nelson and rarely in North I. (from the Urewera National Park and from the headwaters of the Ngaruroro River, Kaweka Range), 500–900 m.

Habitat ecology: *Pseudocyphellaria margaretiae* is a subalpine species epiphytic on the following phorophytes: *Kunzea ericoides, Leptospermum scoparium*, *Nothofagus fusca*, *Olearia avicennifolia*, and *Pseudopanax crassifolius*. It tolerates moderate shade in areas of high rainfall and humidity. On the shores of Lake Rotoiti (Nelson Lakes National Park) at West Bay, and on the Peninsula Walk, it is found on the peeling bark of *Kunzea ericoides* and *Leptospermum scoparium* often close to the ground. It associates with the following lichens: *Anzia jamesii*, *Leioderma amphibolum*, *L. applanatum*, *Nephroma cellulosum*, *N. lepidophyllum*, *N. rufum*, *Pannoparmelia angustata*, *P. wilsonii*, *Pseudocyphellaria crassa*, *P. colensoi*, *P. coronata*, *P.*

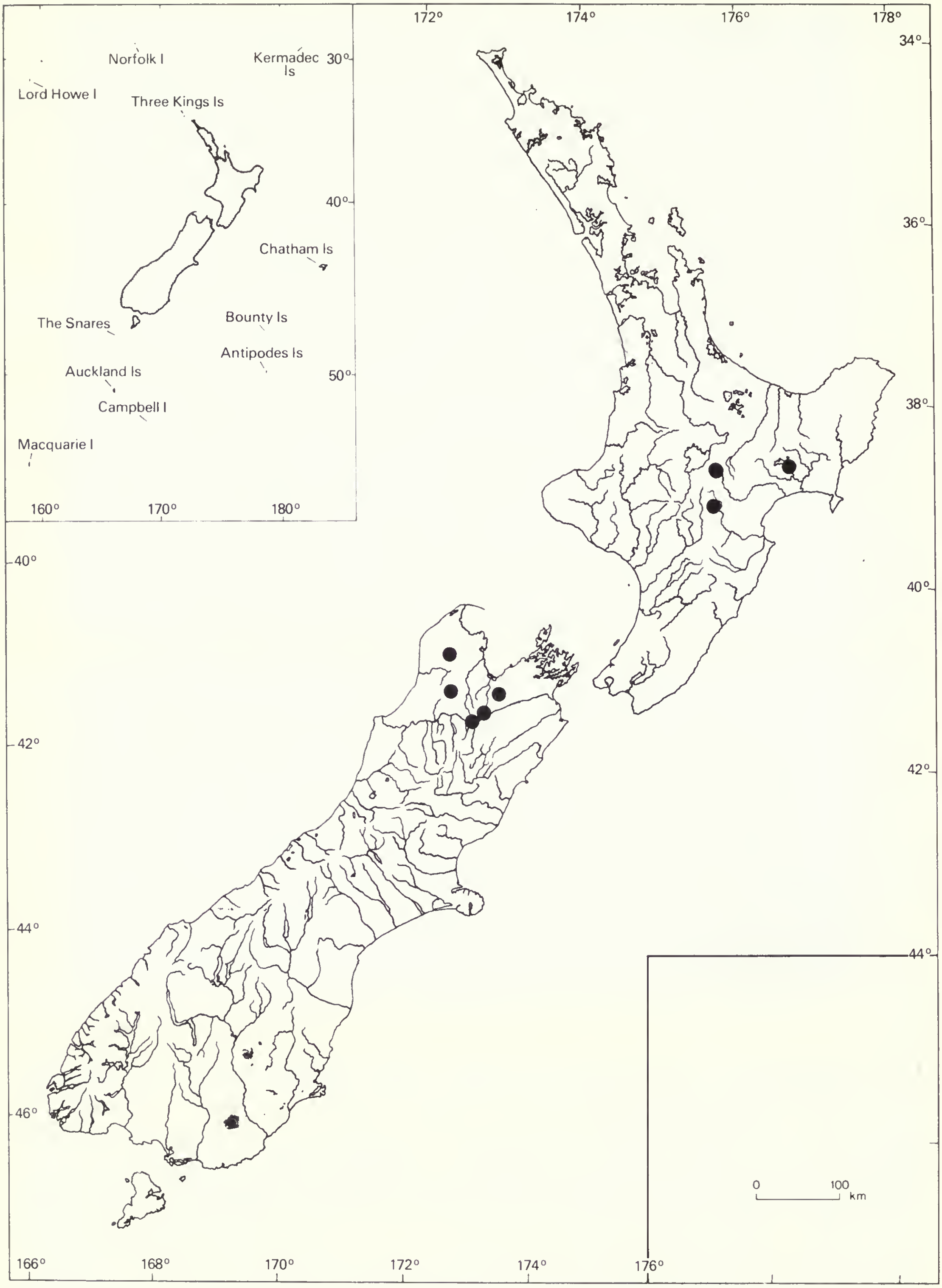
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Fig. 96 Distribution of *Pseudocyphellaria margaretiae*.

granulata, *P. pubescens*, *P. rubella*, *Psoroma euphyllum*, *P. durietzii*, *P. pallidum*, *P. sphinctrinum*, *Sticta limbata*, *S. fuliginosa*, *Usnea capillacea*, and *U. pusilla*.

Specimens examined: 12 [see also Renner & Galloway (1982: 204)].

36. Pseudocyphellaria montagnei (Church. Bab.) D. Galloway & P. James **Fig. 97**

in *Lichenologist* **12**: 300 (1980). – *Sticta montagnei* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 284 (1855). – *Ricasolia montagnei* (Church. Bab.) Nyl., *Syn. meth. lich.* **1**: 373 (1860). – *Stictina montagneana* (Church. Bab.) Nyl. *in* Shirley in *Proc. R. Soc. Qd* **6**: 21 (1889). – *Lobaria montagnei* (Church. Bab.) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21**(3/13): 42 (1896). Type: New Zealand, sine loco, Dr S. [*Dr Andrew Sinclair*] (BM! – lectotype) [see note 1].

Stictina astictina Nyl., *Lich. N.Z.*: 30 (1888*b*). – *Sticta astictina* (Nyl.) Hellbom in *Bih. K. svenska. Vetensk.-Akad. Handl.* **21**(3/13): 33 (1896). – *Pseudocyphellaria astictina* (Nyl.) Magnusson in *Acta*

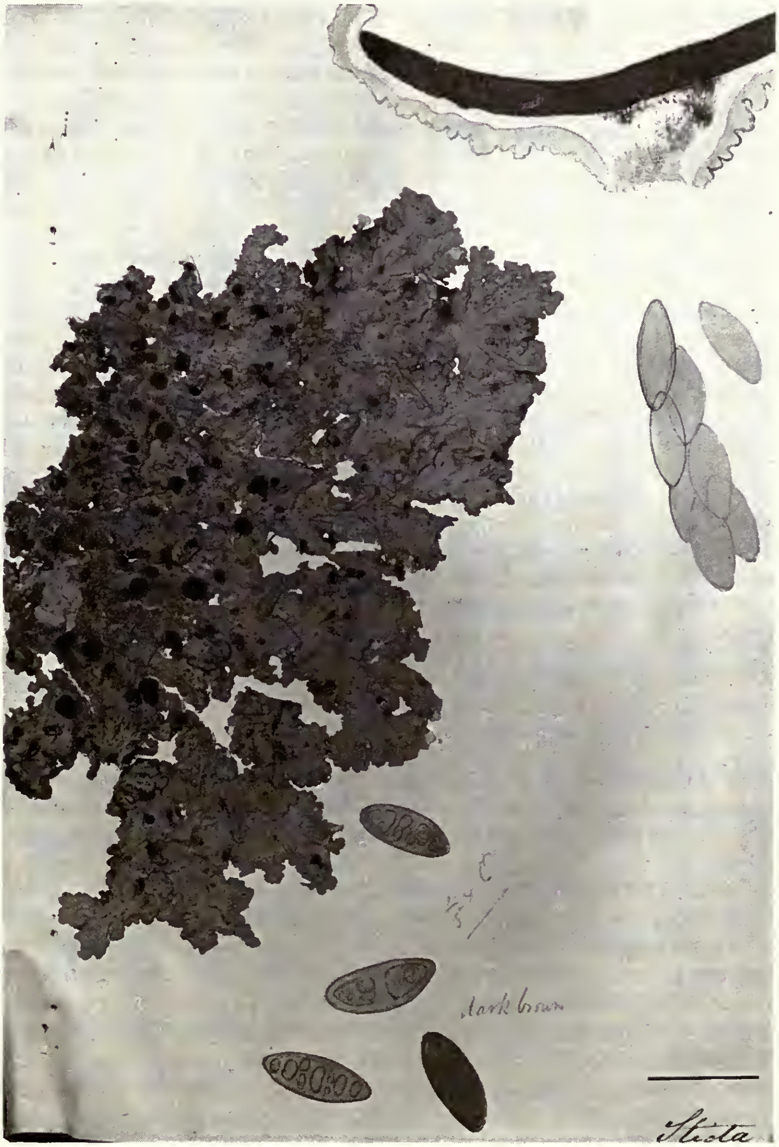


Fig. 97 *Pseudocyphellaria montagnei. Knight*, sine loco (WELT). Scale = 2 cm.

Horti gothoburg **14**: 7 (1940). Type: New Zealand, sine loco (on *Leptospermum*), *R. Helms* 66 (H-NYL 33987! – lectotype; WU! – isotype).

Ricasolia luridescens Stirton in *Trans. N.Z. Inst.* **30**: 393 (1898). – *Lobaria luridescens* (Stirton) Zahlbr., *Cat. Lich. Univ.* **3**: 307 (1925). Type: New Zealand, near Wellington, *J. Buchanan* (BM! – lectotype) [see note 2].

Note 1: *Sticta montagnei* Church. Bab.
Lectotype material of *S. montagnei* (BM) is annotated by J. D. Hooker in ink 'New Zealand Dr S. cf *S. herbacea*' and in pencil by Thomas Taylor '*Sticta glabra* Tayl.'. Babington has added to the label 'This is a form of *S. crocata*! the almost obsolete cyphellae are certainly golden; you have much finer specimens'. In his account of New Zealand species of *Sticta*, Babington (1855: 284) proposed the section *Pseudosticta* Bab. ['Cyphellae wanting altogether, or only occasional'] to accommodate three taxa, *S. montagnei* and two others, *S. herbacea* and *S. glomulifera* [both probably referable to *Lobaria adscripta* (Nyl.) Hue]. Of *S. montagnei* he wrote 'After a good deal of hesitation and consideration, I incline to Dr. Hooker's view, that this Lichen must be compared with *S. herbacea*, which it resembles on many accounts, but is at the same time most abundantly distinct. The apothecia are those of a *Sticta*, bursting from under the gonimic stratum, and remarkable for their crown-bearing leafy margin, which is singularly inflexed, so as often to conceal the disc in great measure. Sporidia minute, contained in elongated asci, subfusiform, not very regular in form, brown, not containing septa, so far as I could observe. The thallus also sometimes has manifest traces of cyphellae, but other specimens would lead any one to consider them a *Parmelia*, as Dr. Montagne was disposed to do, to whom I dedicate the plant, which seems to be undescribed'. Nylander (1860*b*: 373) originally placed *S. montagnei* in the genus *Ricasolia* since he could detect no pseudocyphellae in specimens available to him. *Ricasolia montagnei* was recorded from Otago from collections of W. Lauder Lindsay (Nylander, 1866; Lindsay, 1869). That this diagnosis was in error was soon recognized by Nylander (1867: 439) who noted '*Ricasolium Montagnei* . . . jugendam esse cum *R. adscripta*, specie distincta a *R. herbacea*.' The Otago material cited by both Nylander and Lindsay is referable to *Lobaria asperula* (Stirton) Yoshimura (Galloway, 1981*b*) rather than to *L. adscripta* (Nyl.) Hue, since only *L. asperula* has 'Its margin, as well as the exciple of the apothecia . . . sometimes covered with isidioid or squamulose growths' (Lindsay, 1869: 508). After noting his error in the interpretation of *R. montagnei*, Nylander then gives the following diagnosis 'Definitio *Ricasoliae Montagnei* (Bab.) est haec: thallus glaucus vel passim glauco-rufescens leviter corrugatus vel obsolete scrobiculato-inaequalis aut sublaevis (latit. 12–24 centim.) tenuiter membranaceus (crassit. 0·10–0·12 millim.) lobis crenatis (margine interdum squamulas gerentibus), subtus fusco-nigricans versusque ambitum pallidus, nudiusculus vel versus ambitum leviter arachnoideo-tomentellus; apothecia nigra (latit. 2–6 millim.) sparsa, saepe conferta, margine receptaculari inflexo (saepe laciniato-coronato); sporae fuscae breviter fusiformes 2-loculares vel 1-septatae (physciomorphae), longit, 0·024–·031 millim. – Thallus hypochlorite calcico rose tingitur. Pseudocyphellae incertae minutae subclausae. Cephalodia pyrenodea parca. Spermogonia prominentiis thallinis parum prominulis pagina supera (nec infra)', a description he reprinted the following year (Nylander, 1868*b*: 505).

Note 2: *Ricasolia luridescens* Stirton
The lectotype material (BM) is from James Stirton's herbarium but lacks Stirton's own characteristic manila label. A transcription of his label is made on the BM sheet by A. L. Smith (in pencil) and states 'Sp. 8, fuscae fusif-ellips. 1-sep. interdum (solum) polaribi., 22–28 × 8–10 μ. Apices paraphysarum fusci, clavati K+ violacei. Closely allied to R. montangei'. The specimen is also annotated *Sticta Montagnei* Bab., by Zahlbruckner and carries in addition a note from Mackenzie Lamb 'I took a portion of the specimen to Vienna in 1936 and gave it to Zahlbruckner, who made the above pronouncement. I.M.L.!'.

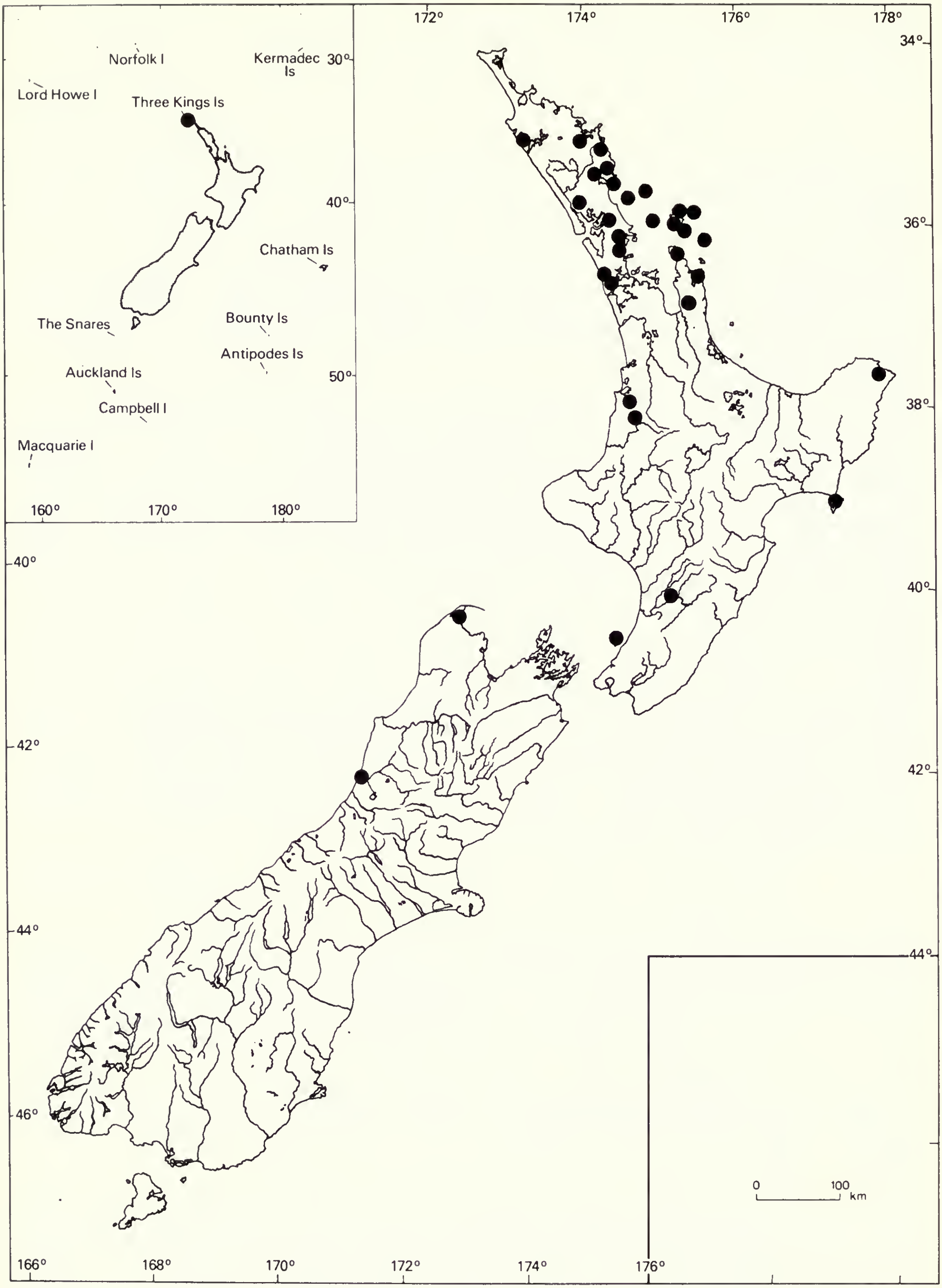
Morphology: Thallus orbicular to irregularly spreading, irregular rosettes often coalescing to form extensive clones, 10–20(–30) cm diam., closely attached centrally, and at margins, corticolous, rarely saxicolous. *Lobes* broad, rounded, 3–8(–15) mm wide and to 4 cm long, radiating, ± discrete to contiguous at margins, complex-imbricate centrally. *Margins* undulate-sinuous, not noticeably ascending, rather closely attached to substrate, rarely entire, normally notched, incised or ± crenate, at length strongly squamiform-phyllidiate. *Upper surface* olive greenish, margins suffused red-brown when wet, pale glaucous or greyish buff when dry; undulate to strongly ridged, pitted, plicate-glomerulate, often ± faveolate towards lobe margins, hemispherical pycnidia and/or cephalodia often present, ± phyllidiate, matt, without isidia, soredia, maculae or pseudocyphellae. *Phyllidia* sparse to frequent and then often completely obscuring thallus, marginal and laminal, squamiform, distinctly dorsiventral, complexly divided, lower surface at length developing short tomentum and occasionally minute, white pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* pale yellowish buff at margins, brownish centrally, shallowly wrinkled or minutely papillate, scattered hemispherical cephalodia only truly prominent feature, glabrous or scattered tomentose, tomentum very thin, velvety, pale buff to dark brown. *Pseudocyphellae* white, inapparent, sparse to frequent, sometimes densely developed, crowded, minute (to 0·1 mm diam.), papillate, concolorous with lower surface, decorticate area often not fully exposed, very inconspicuous, white, flat. *Apothecia* sparse to frequent, laminal and marginal, round to irregularly undulate, 0·5–5(–9) mm diam., sessile, constricted at base or very shortly pedicellate, pedicel narrow, disc dark red-brown when wet, ± black when dry, matt, epruinose, imperforate, exciple prominent, persistent, pale yellowish buff, completely obscuring disc in young fruits, strongly verrucose-areolate, flaking in small scales near margins in older fruits, margins inrolled, scalloped, striate-lacerate to sparsely or densely phyllidiate. *Pycnidia* common, flattened-hemispherical, to 0·5 mm diam., apical ostiole red-brown, punctiform, 0·1 mm diam., often with a pale or whitish surrounding halo.

Anatomy: Thallus 70–100(–140) μm thick. *Upper cortex* 18–22 μm thick, outermost 10–12 μm pale orange-brown or yellowish brown, lower zone abutting photobiont layer, colourless, cells 4–7 μm diam. *Photobiont layer* 11–13·5 μm thick, *photobiont* green, cells round to irregular, 4–6·5 μm diam. *Medulla* 28–45(–90) μm thick, hyaline to pale straw. *Lower cortex* 9–12 μm thick, 2–3 rows of cells 2–4·5 μm diam., lower part of cortex pale yellow to red-brown, innermost layer adjacent to medulla colourless. *Tomental hairs* sparse, 4–5 μm thick, simple, septate, colourless, solitary or 3–5-together in thin fascicles, 25–55 μm long. *Apothecia: Exciple* 70–90 μm thick, outermost 20–25 μm pale yellow-brown, inner zone hyaline, in older parts, exciple separated from hypothecium by a well-developed medulla with a narrow layer of photobiont cells between cells of exciple and medulla; in older parts of exciple, pyramidal clusters of cells (10–30 cells wide) separate from each other giving an areolate-scabrid appearance to exciple, and rarely, rows of cells extend beyond exciple as short hairs. *Hypothecium* 50–75 μm thick, yellow-brown to dark red-brown. *Thecium* 110–140 μm tall, pale straw; *epithecium* 6·5–11 μm thick, pale yellow-brown to dark red-brown or grey-brown, distinctly granular, turning purple-violet in K; *paraphyses* ± moniliform (3–5 cells) at apices. *Asci* 72–80 × 18–23 μm. *Ascospores* simple, colourless at first, becoming smoky grey at maturity, oval-ellipsoid with pointed ends, 1-septate, thickened, locules ± equal, septum 3–4 μm thick, walls 1–2 μm thick, at maturity two irregular polar locules are split off from two large central locules forming 3-septate spores, 18–25(–27) × 9–11 μm.

Chemistry: Methyl evernate, tenuiorin, methyl lecanorate, methyl gyrophorate, evernic acid, gyrophoric acid, hopane-6α, 7β, 22-triol, norstictic (tr.), stictic, cryptostictic (tr.), constictic, hypostictic (tr.), and hyposalazinic (tr.) acids.

Distinguishing features: Pseudocyphellaria montagnei has a white medulla, green photobiont, minute, sparse pseudocyphellae on the lower surface which itself is often ± glabrous or largely devoid of tomentum conferring a pale, *Lobaria*-like appearance, laminal phyllidia often copiously developed and obscuring thallus, and phyllidiate margins to the apothecia which have dark-brown to black discs. It has a characteristic chemistry being related to both that of *P. durietzii* and *P. hookeri*, and also to *P. physciospora*, and characterized by a wide range of depsidones (including gyrophoric acid which gives a fleeting C+ red reaction to the upper surface when dry, and more especially to the lower surface) and hopane-6α, 7β, 22-triol.

Variation: Major variation in this species resides in two characters: the pseudocyphellae of the lower surface which are often poorly developed with only a very small decorticate area visible (this apparent lack of pseudocyphellae caused some earlier authors to place this species in either *Lobaria* or *Ricasolia*), and the numbers & position of phyllidia on the upper surface, ranging from collections without phyllidia to those in which the development of phyllidia is so dense that the thallus is obscured. Chemically the species is close to *P. durietzii*, *P. hookeri*, and *P.*


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
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44°
46°
166°
168°
170°
172°
174°
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Fig. 98 Distribution of *Pseudocyphellaria montagnei*.

physciospora. It is distinguished from *P. hookeri* by its non-faveolate upper surface, development of superficial phyllidia, and the green photobiont. It is separated from *P. durietzii* by the marginal and laminal phyllidia, the phyllidiate apothecial margins, the non-faveolate upper surface, and in the morphology of the lower surface and of the pseudocyphellae. *P. physciospora* differs from *P. montagnei* in having a faveolate upper surface, lacking phyllidia, and having yellow pseudocyphellae on the lower surface.

Distribution: (Fig. 98) From the Three Kings Is (lat. 34°S) southwards to Kapiti I., in North I., in mainly coastal habitats but inland at Mangaotaki near Pio Pio in the King Country, and to the Manawatu near Palmerston North. In South I., from north-west Nelson (Kaihoka Lakes) to Greymouth [material of *Stictina astictina* collected by Richard Helms may well have come from Greymouth, since it is known that in the 1880s he was a jeweller in this Westland town and many other specimens of *Pseudocyphellaria* and other lichens collected by him from this area and from the Paparoa Range at this time are present in several European herbaria, especially at MANCH, W, and WU]. *P. montagnei* is known from the following offshore islands: Three Kings Is, Hen I., Lady Alice I., Little Barrier I., Great Barrier I., Rakitu I., Cuvier I., and Kapiti I. A collection made by Sir Everard Home in 1853 from the Auckland Is (BM) is in error and undoubtedly refers to Auckland (town or province) and not to the subantarctic islands named after Lord Auckland. Collections made by David Lyall (BM) from Middle Island (South I.) are unlocalized.

Habitat ecology: Pseudocyphellaria montagnei is an epiphyte of northern coastal forest trees and shrubs, being known from the following phorophytes: *Avicennia marina* var. *resinifera*, *Bielschmiedia taraire*, *Coprosma repens*, *Cordyline australis*, *Corynocarpus laevigatus*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *D. intermedium*, *Dicksonia fibrosa*, *Dysoxylum spectabile*, *Kunzea ericoides*, *Leptospermum scoparium*, *Myrsine australis*, *Pittosporum crassifolium*, *Podocarpus totara*, *Rhopalostylis sapida*, and *Vitex lucens*. It also spreads over decaying logs and rocks below such phorophytes when light is sufficient, and it has also been collected from rock in papa cliffs. It is a photophilous species and is not found in deep shade where it is unable to compete with species having blue-green photobionts, or with faster growing mosses and hepatics. It associates with mainly northern lichens including species of *Heterodermia*, *Leioderma duplicatum*, *L. erythrocarpum*, *Pannaria elatior*, *Parmotrema cetratum*, *P. grayanum*, *P. tinctorum*, *Pseudocyphellaria aurata*, *P. carpoloma*, *P. chloroleuca*, *P. poculifera*, *Ramalina australiensis*, *R. pacifica*, *R. peruviana*, *Psoroma araneosum*, *P. allorhizum*, *Sticta babingtonii*, *S. squamata*, and *Teloschistes flavicans*.

Specimens examined: 55.

Exsiccata seen: Lojka, *Lichenotheca Universalis* Fasc. III, No 114 (1886). [Nova Zelandia, leg. C. Knight, sub *Ricasolia montagnei*, BM!, G!, M!, UPS!, W!]. Also No 118, sub, *Sticta multifida* G!

37. **Pseudocyphellaria multifida** (Nyl.) D. Galloway & P. James **Fig. 99**

in *Lichenologist* **12**: 301 (1980). – *S. multifida* Nyl., *Syn. meth. Lich.* **1** (2): 363 (1860). – *S. dissecta* Laurer in *Linnaea* **2**: 41 (1827), non *S. dissecta* (Sw.) Ach. [*Meth. Lich.*: 279 (1803)] (Art. 64.1). – *Crocodia multifida* (Nyl.) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Lobaria multifida* (Nyl.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 38 (1896) 1896). Type: Nov. Holland (Australia), *Sieber* 45, ex Herb. Churchill Babington (BM!-lectotype) [see note 1].

Sticta subvariabilis Nyl. in *Flora, Jena* **50**: 439 (1867). – *Lobaria subvariabilis* (Nyl.) *Hellbom in Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 41 (1896). – *Pseudocyphellaria subvariabilis* (Nyl.) Vainio in *Philipp. J. Sci. C* **18**: 116 (1913). – *Cyanisticta subvariabilis* (Nyl.) Dodge in *Nova Hedwigia* **19**: 490 (1971). Type: New Zealand, sine loco, *C. Knight* 1867 (H-NYL 33465!-holotype).

Sticta psilophylla f. *amphicarpa* Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31**: 30 (1892). Type: New Zealand, sine loco, 1883, *Dr Knight* (G 002003!-holotype) [see note 2].

Note 1: *Sticta multifida* Nyl.
Nylander (1860*b*: 363) proposed *Sticta multifida* for *S. dissecta* Laurer, realising that Laurer's name was a

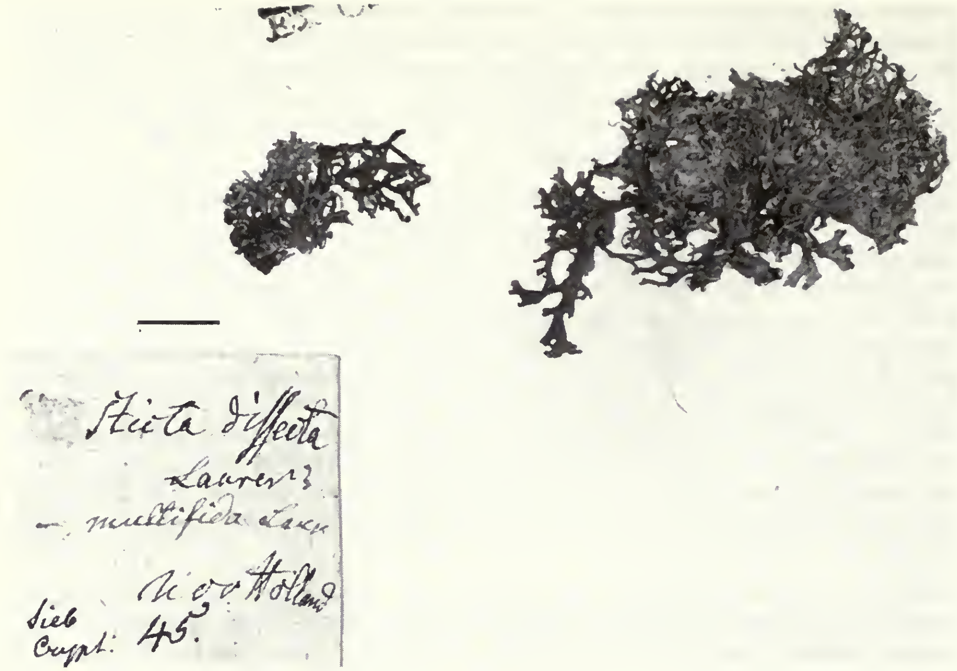


Fig. 99 *Pseudocyphellaria multifida*. Lectotype of *Sticta dissecta* Laurer (BM). Scale = 1 cm.

later homonym of *S. dissecta* (Sw.) Ach. This latter taxon (correctly *Lobaria dissecta* (Sw.) Räuschel) he discussed under *Ricasolia* (Nylander 1860*b*: 370).

Laurer may also have recognised his error in naming an Australian lichen *Sticta dissecta*, since he labelled specimens seen by Nylander (1860*b*:363), and by Krempelhuber (1868: 318–319 tab. IV fig. 2 a-b) as *Sticta multifida*, the name later taken up by Nylander. A specimen collected by Sieber (No. 45) from New Holland, in Churchill Babington's herbarium (BM) is labelled 'Sticta dissecta Laurer-multifida Laurer. Sieb. Crypt.:45', apparently in Laurer's handwriting (Fig. 99). This is chosen as the lectotype of *S. dissecta* Laurer and *S. multifida* Nyl.

Authentic material of Sieber no. 45 from New Holland was examined in BM, G, L, PC-LENORMAND and PC-THURET. In both Delise's and Bory de St Vincent's herbaria (PC-LENORMAND and PC-THURET respectively) material of Sieber no. 45 is annotated as a juvenile state of *Sticta billardierei* Delise. A specimen labelled *Sticta billardierei* in Montagne's herbarium (PC-MONTAGNE) collected in 'Nouv. Holl.' by La Billardière and given to Montagne by Philip Barker Webb, is also referable to *Pseudocyphellaria multifida*. Nylander's use of *Sticta multifida* was misunderstood by Galloway *et al*. (1983: 141) when they proposed use of *Pseudocyphellaria subvariabilis* (Nyl.) Vainio (see also Galloway 1985b: 459; 1986*b*).

Note 2: *Sticta psilophylla* f. *amphicarpa* Müll. Arg.
Holotype material of *Sticta psilophylla* f. *amphicarpa* (G 002003) consists of two specimens glued to a small sheet. The left-hand specimen is fertile and is *Pseudocyphellaria multifida* admixed with a small fragment of *P. chloroleuca* (C+ red). The right-hand specimen is *P. chloroleuca* and is sterile. Müller Argoviensis has arrowed the left-hand specimen and added the annotation 'amphicarpa!'. This refers to the fact that well-developed apothecia are present in this specimen both on the upper surface and also on the lower surface, a rather rarely observed phenomenon.

Morphology: Thallus very variable in thickness and in lobe morphology, primarily in the number, size, and shape of phyllidia, rather small, delicate, 2–10(–15) cm, rarely to 20 cm diam., irregularly spreading, rather loosely attached, margins free and often ascending, corticolous, muscicolous, terricolous, and saxicolous. *Lobes* narrow, 1–5 mm wide, rarely to 15 mm wide, usually complexly branched, entangled-imbricate, ± discrete at margins, densely imbricate centrally. *Margins* sinuous or ragged, dentate-incised to ± richly phyllidiate, smoothly rounded, slightly thickened below and occasionally also ridged above, without pseudocyphellae, sinuses well-developed, semicircular. *Upper surface* bright lettuce-green to dark emerald-green, occasionally suffused brownish at apices when moist, pale greenish grey to buff-brown on long storage when dry, undulate, occasionally shallowly wrinkled or pitted, in places minutely white-papillate (×10 lens), smooth, matt or glossy, cephalodia also visible as hemispherical (0·2 mm diam.) swellings, sometimes ± coriaceous, tough, without soredia, isidia or pseudocyphellae. *Maculae* occasional, best seen towards lobe apices or margins, white, scattered, effigurate. *Phyllidia* occasional to common, often densely developed and obscuring thallus, marginal or sometimes regenerating from cracks in upper surface, flattened, ± dorsiventral, constricted at base, lower surface with minute, white pseudocyphellae and occasional wisps of tomentum, rarely at first subterete and palmate-coralloid, simple to richly divided, squamiform to strap-like, often ± brown-tipped, never tomentose at margins. *Medulla* white. *Photobiont* green. *Lower surface* whitish, pale pinkish white to pale yellowish buff or brownish and ± glabrous at margins, darker centrally, smooth or shallowly wrinkled, puckered, grooved or papillate, internal cephalodia visible as distinctive swellings, concolorous with lower surface, with irregular scattered tomentum centrally, rarely tomentose from margins to centre, tomentum thin, soft, white, short and velvety, often patchily developed and ± tufted, frequently extensive glabrous patches occur. *Pseudocyphellae* white, scattered, fleck-like, most noticeable at margins, round to irregular, 0·1 mm diam. or less, occasionally to 0·5 mm, flat or very shallowly papillate, decorticate area flat or subconcave. *Pycnidia* occasional to frequent, marginal and laminal, scattered, punctiform, 0·1 mm diam. or less, red-brown, often clustered, eroding, and leaving small pits. *Apothecia* rare or absent to occasional, solitary to 3-5-clustered often ± obscured by phyllidia, marginal and laminal, sessile, constricted at base, 0·5–4·5 mm diam., round to irregular, or contorted through mutual pressure, concave at first, plane, undulate to subconvex at maturity, disc pale to dark red-brown, margins crenate-striate, ± persistent, or excluded in very mature fruits, matt, smooth to slightly roughened-papillate, epruinose, exciple whitish to pale buff or brownish, translucent when wet, scabrid-areolate.

Anatomy: *Thallus* 174–230(–275) μm thick. *Upper cortex* 38–45 μm thick, colourless to pale straw-yellow, cells in upper layer closely packed, 4·5–7 μm diam., cells adjoining photobiont layer larger, more loosely arranged, 9–15·5 μm diam. *photobiont layer* 23–34(–41) μm thick, cells densely packed, layer mainly 23 μm thick but isolated groups of photobiont penetrating into medulla, *Photobiont* green, cells rounded, to 7 μm diam. *Medulla* 73–140 μm thick, colourless. *Lower cortex* 20–25 μm thick, colourless to pale straw-yellow, cells structure as in upper cortex. *Tomental hairs* colourless, 4.5 μm diam., 45–90(–200) μm long, scattered, often sparse, single or in fascicles (2–8). *Apothecia: Exciple* colourless, 120–200 μm thick, cells 9–12 μm diam. *Hypothecium* 90–110 μm thick, hyaline to pale straw-yellow, unchanged in K. *Thecium* 90–100 μm tall, colourless; *epithecium* 7–9 μm thick, yellow-brown, darkening to olive-brown in K, colour in a band 4–5 μm thick below tips of paraphyses. *Asci* 81–94 × 15·5–18 μm. *Ascospores* pale yellow-brown, broadly fusiformellipsoid, 1-3-septate, not thickened, 23–34 × 9–11·5 μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria multifida* is an Australasian species having, as its name suggests, very variable, rather delicate lobes, rarely ± broadly rounded to more usually narrow and highly divided, entangled-imbricate the margins ragged-incised to lobulate or richly phyllidiate. The upper surface is smooth, undulate or shallowly wrinkled, with occasional, white maculae towards margins, and occasional to densely developed, simple, squamiform, palmate-coralloid to ± strap-like phyllidia. It has a white medulla, a green photobiont, and a pale whitish, glabrous, glossy, smooth or shallowly wrinkled lower surface, with a usually poorly developed, thin, short, velvety tomentum centrally, and with scattered, white, fleck-like pseudocyphellae most noticeable at margins. Apothecia rare, often absent, sessile, with a thin, scabrid-areolate exciple ± excluded at maturity. The epithecium is yellow-brown darkening to olive-brown in K. Spores pale yellow-brown, 1-3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)].

Variation: *Pseudocyphellaria multifida* is an extremely variable species with a highly plastic morphology, the lobes varying from broad and rounded with rather few marginal phyllidia (Fig. 100A), to a complex-imbricate crust of highly divided, entangled, narrow phyllidia (Fig. 100B) and often a single plant can show both extremes of development. All forms, are, however, united by the characteristic pale, whitish glabrous, glossy lower surface (especially near the margins), with white, fleck-like pseudocyphellae and often only very poorly developed tomentum. The plasticity of form shown by this species has given rise to confusion over its correct name. For example, in Zahlbruckner (1941) the following records all refer in part to *P. multifida* [see also note 1]: *Sticta dissimulata* var. *multifida*, *S. psilophylla*, *S. polyschista*, *S. montagnei*, *S. episticta*, and *S. fragillima* var. *myrioloba*. Martin (1966, 1969*a*) and Martin & Child (1972) record the nom. nud. *Pseudocyphellaria polyschista* for *P. multifida*.

Pseudocyphellaria multifida is distinct from *P. chloroleuca* which has a glabrous lower surface and fragile, terete marginal and laminal isidia, and a different chemistry (gyrophoric acid

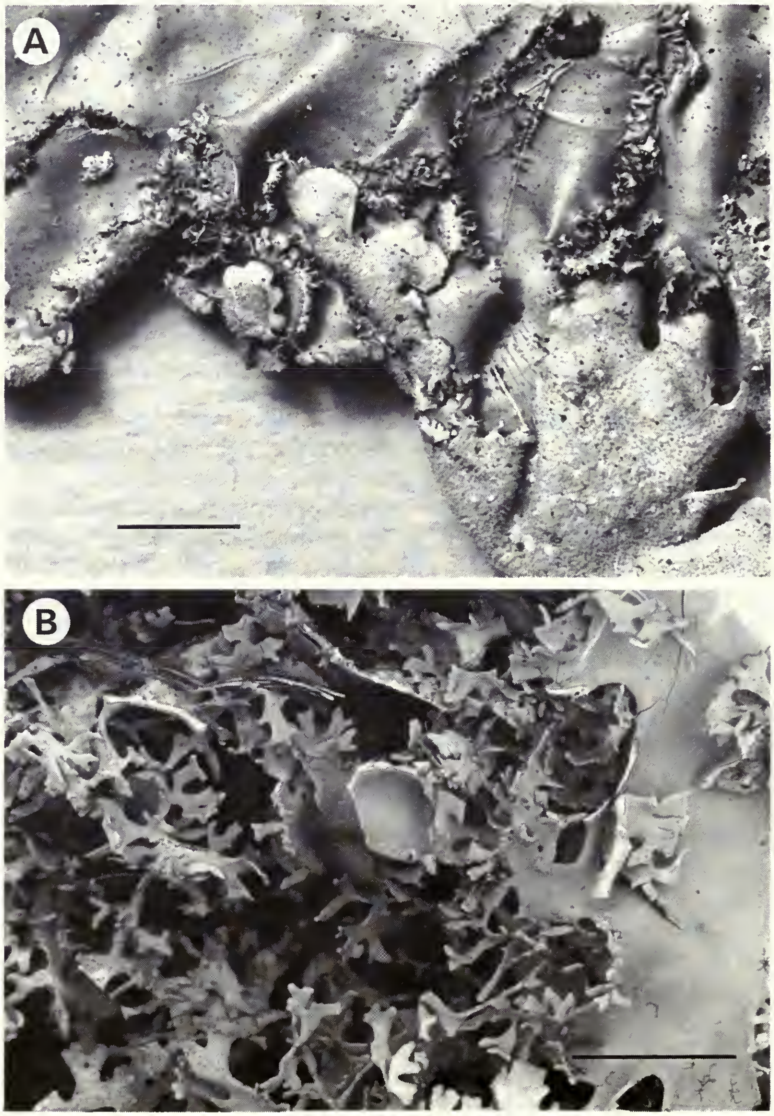
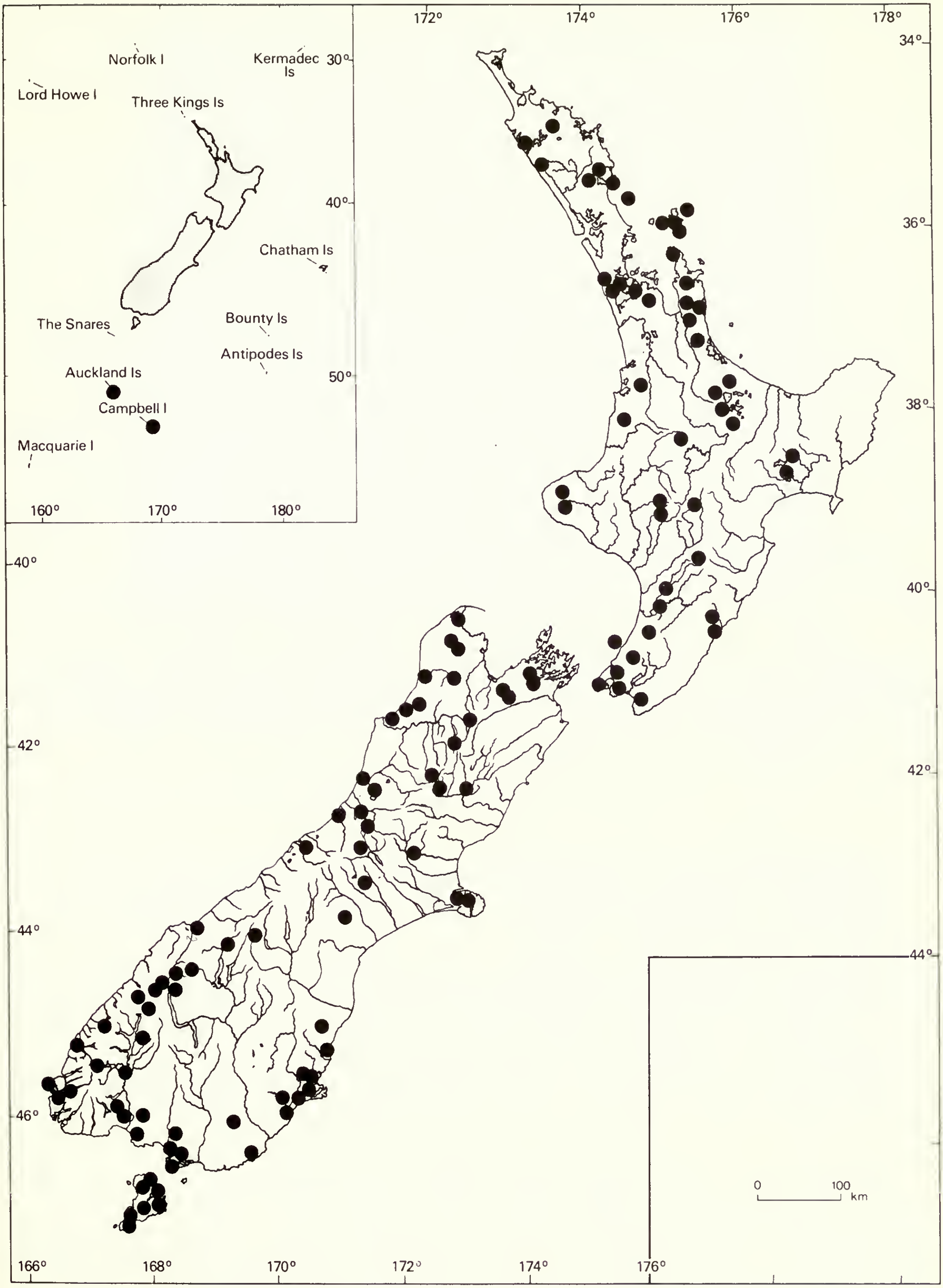


Fig. 100 *Pseudocyphellaria multifida*. A. Totara Reserve, Pohangina Valley, *Allan* V 184 (W). Scale = 5 mm. B. Kaitoke Range, Taranaki, *Tibell* 15062 (UPS). Scale = 4 mm.


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
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50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
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Fig. 101 Distribution of *Pseudocyphellaria multifida*.

reacting C + red on upper and/or lower surfaces); and from *P. fimbriata*, which is a more robust, coriaceous plant, with pubescent marginal phyllidia, and a dark lower surface with prominent white pseudocyphellae. The related *P. wilkinsii* has laminal pseudocyphellae and broader lobes.

Distribution: (Fig. 101) Widespread and common from lat. 35°S in North Auckland to southern Stewart I., lowland to subalpine, sea-level to 1560 m.

Habitat ecology: Pseudocyphellaria multifida grows in a wide variety of habitats, from deep shade on the forest floor, to full sunlight at forest margins and in scrub associations, to subalpine tussock grassland at 1560 m. Although most commonly associated with mosses on tree trunks, it will also colonize fallen logs and mossy boulders in moderate to deep shade, as well as twigs and branches in moderate to high-light habitats. It has a wide altitudinal range, being found from coastal scrub and forest to rain forest close to the Main Divide, and above treeline in subalpine scrub and tussock grassland. It is absent from the driest areas of the country and is best developed in cool, moist, humid sites, being especially luxuriant in forests clothing Mt Egmont in Taranaki, and in the forests of the west coast of South I. In mid altitude forests (200–800 m) west of the Main Divide in South I., it is often the dominant species of *Pseudocyphellaria*.

It is known from the following phorophytes: *Aristotelia serrata*, *Beilschmiedia tawa*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Dracophyllum* spp., *Fuchsia excorticata*, *Griselinia littoralis*, *Leptospermum scoparium*, *Libocedrus bidwillii*, *Metrosideros lucida*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Pittosporum eugenioides*, *Pinus radiata*, *Podocarpus hallii*, *P. totara*, *Pseudopanax arboreus*, *Pseudowintera colorata*, *Quintinia serrata*, *Rhopalostylis sapida*, and *Weinmannia racemosa*.

Pseudocyphellaria multifida associates with the following lichens: *Cladia aggregata*, *Gymnoderma melacarpum*, *Hypogymnia subphysodes*, *Leptogium laceroides*, *Menegazzia pertransita*, *Metus conglomeratus*, *Phlyctella sordida*, *Pseudocyphellaria billardierei*, *P. colensoi*, *P. dissimilis*, *P. faveolata*, *P. glabra*, *P. homoeophylla*, *P. lividofusca*, *P. rufovirescens*, *Psoroma microphyllizans*, *P. pallidum*, *P. sphinctrinum*. *Ramonia* spp., *Siphula decumbens*, *Sphaerophorus patagonicus*, *S. notatus*, *S. ramulifer*, *S. scrobiculatus*, *S. tener*, *Sticta cinereoglauca*, *S. filix*, *S. lacera*, *S. latifrons*, *S. subcaperata*, *Trapeliopsis granulosa*, *Usnea capillacea*, and *U. xanthophana*.

Specimens examined: 250.

38. **Pseudocyphellaria murrayi** D. Galloway **Fig. 102**

in *Mycotaxon* **16**: 205 (1982). Type: New Zealand, North I., South Auckland, Mangaotaki Reserve, King Country, near Pio Pio, on twigs of *Griselinia littoralis* in deep shade, 9 June 1978, *D. J. Galloway* (CHR 343163! – holotype; BM! – isotype).

Morphology: Thallus forming entangled clones of ± strap-like lobes, often ± pendulous, loosely attached centrally, free and ascending at apices, 5–15(–30) cm diam., corticolous. *Lobes* linear-elongate, rather narrow, 2–6(–12) mm wide, attenuating towards apices and there acute, blunt or ± forked, ± subdichotomously branching, discrete near margins, complex-imbricate, entangled centrally. *Margins* entire, subascendent, involute towards apices, rounded, noticeably thickened, often somewhat longitudinally ridged or puckered, suffused red-brown, with occasional, punctiform to ± linear, white pseudocyphellae. *Upper surface* dark slate-blue suffused red-brown at margins and apices, pale grey-green, suffused red-brown at apices and margins when dry, smooth, glabrous, matt or shining, sometimes minutely punctate-impressed or wrinkled, undulate, rarely very shallowly faveolate towards apices, ridges indistinct, without soredia, isidia, pseudocyphellae or phyllidia. *Maculae* white, often conspicuous, scattered, effigurate, occasionally coalescing to form white, cyanobiont-free patches. *Medulla* white. *Photobiont Nostoc*. *Lower surface* pale or white and ± glabrous at lobe apices, wrinkled-bullate, often ± pale buff and uniformly tomentose from margins to centre, tomentum regular, rather short, arachnoid. *Pseudocyphellae* scattered, sparse to moderately common, round to irregular, intense white, 0·1–0·2(–0·8) mm diam., margins very thin, sometimes ± raised, decorticate area

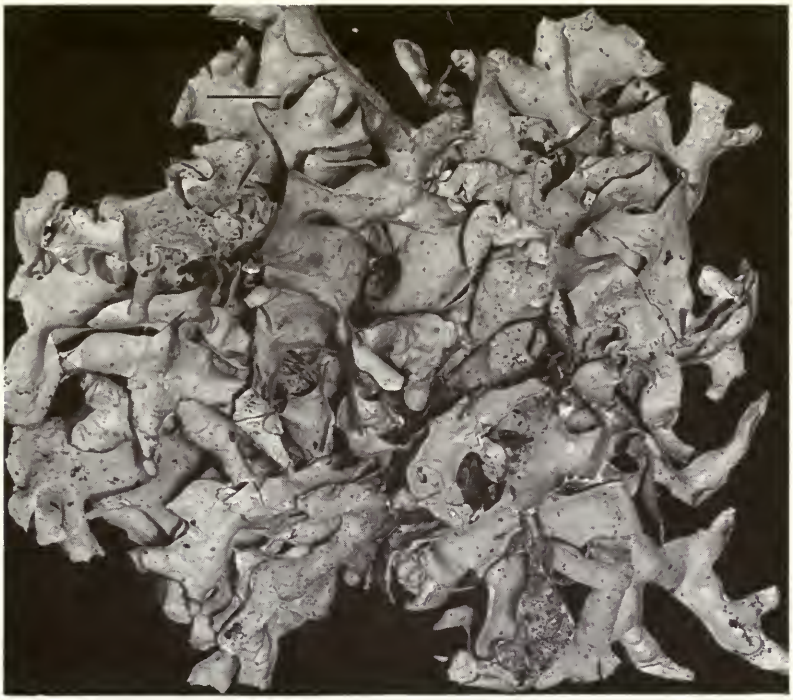

Fig. 102 *Pseudocyphellaria murrayi*. Moerangi, *Bartlett* (BM). Scale = 1 cm.

flat or slightly concave, sunk in tomentum or slightly projecting above. *Pycnidia* common to rare, congregated on ridges or near margins, rarely ± solitary on lamina, usually several clustered closely together, hemispherical, 0·1–0·2 mm diam., ostiole red-brown, punctate-impressed. *Apothecia* very rare (only seen once), marginal, sessile to subpedicellate, 1–5 mm diam., plane at first then shallowly convex to deeply undulate, disc pale to dark red-brown, matt, slightly shining, epruinose, margins pale buff-pink, scabrid, roughened, excluded at maturity, exciple pale pinkish-buff, areolate-scabrid.

Anatomy: *Thallus* 130–230(–270) μm thick. *Upper cortex* 27–35 μm thick, uppermost 7–9 μm ochre-brown, remainder pale straw-yellow, cells 3·5–9 μm diam. *Photobiont layer* 45–56(–63) μm thick, *photobiont Nostoc*, cells 2·5–4·5 μm diam. *Medulla* 45–74 μm thick, colourless. *Lower cortex* 22–27 μm thick, pale straw-yellow, cells 4–9 μm diam. *Tomental hairs* colourless, to 5 μm diam., 45–90(–180) μm long. *Apothecia*: *Exciple* colourless, outer layers pale yellow-brown to pale straw-yellow, cells 7–13.5 μm diam. *Hypothecium* 36–45 μm thick, yellow-brown to pale straw-yellow, unchanged in K. *Thecium* colourless or pale straw-yellow, 70–90 μm tall; *epithecium* 11·5–14 μm thick, yellow-brown to red-brown, turning olive-brown in K or ± unchanged, outer surface irregular, overlain by a thin (7 μm), amorphous, colourless gel; *paraphyses* submoniliform at apices. *Asci* 73–85 × 13·5–18 μm. *Ascospores* yellow-brown, oval-ellipsoid, 3-septate, apices rounded or pointed, contents distinctly vacuolate, 23–27 × 7–9 μm.

Chemistry: 7β-acetoxyphopan-22-ol, and hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria murrayi* is a rather restricted endemic species having linear-elongate, rather narrow lobes, ± subdichotomously branching, with entire margins and lacking soredia, isidia or phyllidia. The upper surface is smooth, glabrous, wrinkled, punctate-impressed to shallowly faveolate. It has a white medulla, a blue-green photobiont, and a pale, wrinkled-bullate lower surface with a short, regular, pale tomentum and scattered white pseudocyphellae. Apothecia are extremely rare, sessile to subpedicellate, the

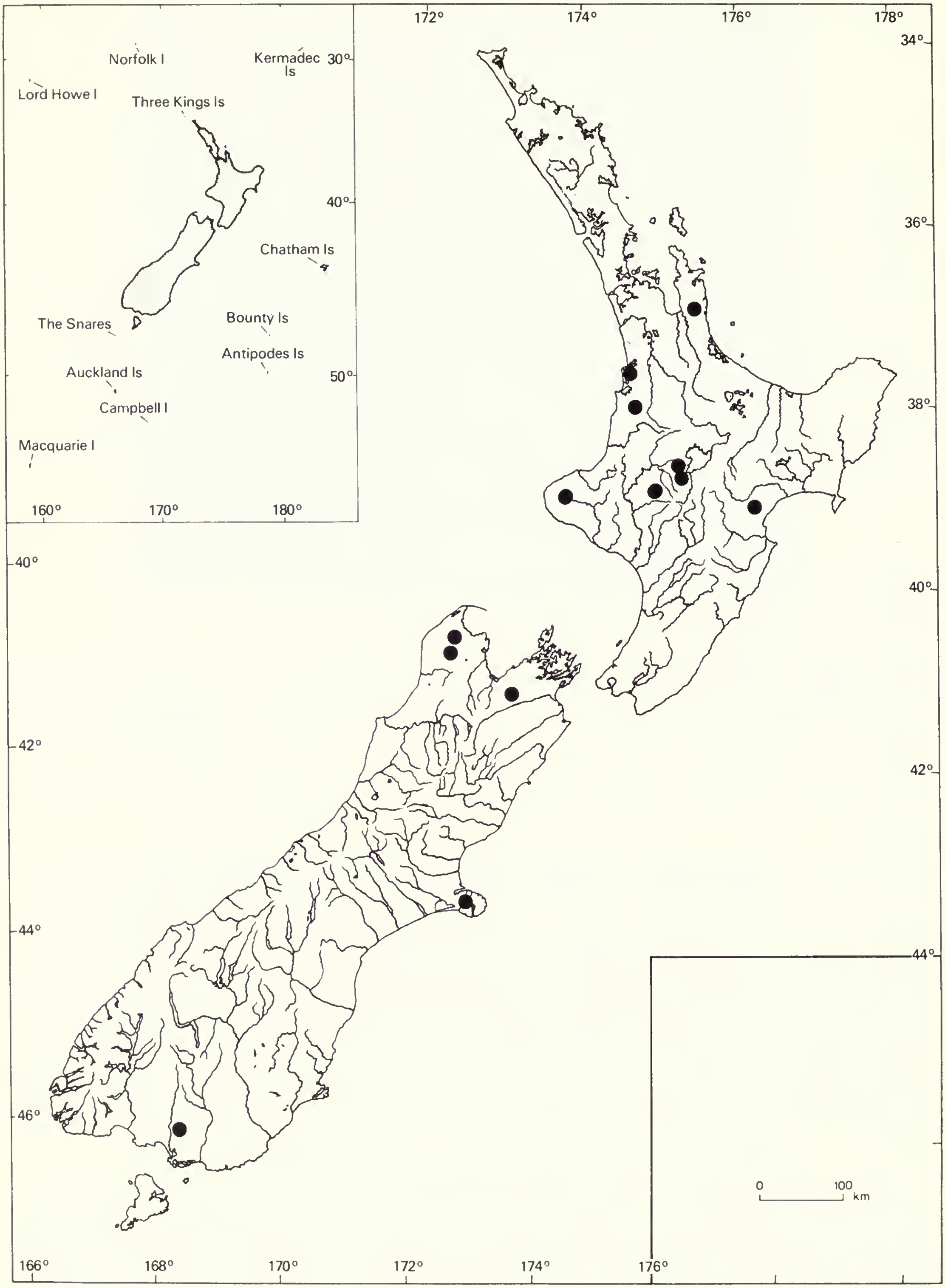
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Fig. 103 Distribution of *Pseudocyphellaria murrayi*.

disc dark red-brown, the exciple scabrid-roughened, pale pinkish buff, excluded at maturity. Spores are yellow-brown, over-ellipsoid, 3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)].

Variation: *Pseudocyphellaria murrayi* is a still poorly collected species and specimens examined show little morphological variation except in the degree of tomentum on the lower surface. Tomentum is always present centrally and often also at the lobe margins as well, but may be absent from lobe apices. It is closely related chemically and morphologically to *P. rufovirescens* and the two taxa form photosymbiodemes (Renner & Galloway, 1982) with attached thalli, known from the Mangaotaki River, Kuratau Clearing, Moerangi in North I., and from Mt Glasgow (Nelson) and Banks Peninsula in South I. When growing independently it is distinguished from *P. rufovirescens* by the smoother, undulate, but seldom faveolate lobes which are expanded at the apices, the leaden-grey colour when wet because of the presence of the blue-green photobiont, the consistent development of a ± uniform tomentum on the lower surface, and the dark red-brown apothecical discus with corrugate-striate or verrucose margins. In *P. rufovirescens*, tomentum on the lower surface is very rudimentary and ± restricted to central parts of mature lobes, the margins and apices being regularly glabrous, white, and shining. The pseudocyphellae of *P. rufovirescens* are also smaller, more pock-like, and scattered and not conspicuous and large as they are in *P. murrayi*. *P. murrayi* differs from *P. cinnamomea* which has narrow, strap-like lobes which are ± canaliculate and ± costate below and which has gyrophoric acid in the medulla.

Pseudocyphellaria murrayi is named for the late Dr James Murray (1923–1961) of the Chemistry Department, Otago University, Dunedin, New Zealand, who first became interested in New Zealand's lichens through his chemical studies on *Pseudocyphellaria*. He was engaged in monographing *Sticta* and *Pseudocyphellaria* at the time of his death (June, 1961), and made the first collection of *P. murrayi* from Forest Hill, Southland, in January 1957.

Distribution: (Fig. 103) North I., from Kauaeranga River (lat. 37°S), near Raglan, and the Mangaotaki Valley (South Auckland), near Tutira (Hawke's Bay) and Erua Swamp (Wellington). In South I., from Red Hills, Mt Glasgow, and Cobb Ridge (Nelson), Banks Peninsula (Mt Sinclair Reserve), and Forest Hill (Southland), lowland to subalpine, 150–900 m.

Habitat ecology: *Pseudocyphellaria murrayii*, although rather rare and local, has a wide distribution in New Zealand. It is found in areas of high humidity and moderate to dense shade on the following phorophytes in mainly lowland areas: *Dracophyllum subulatum*, *Griselinia littoralis*, *Leptospermum scoparium*, *Nothofagus menziesii*, *Myrtus bullata*, *Podocarpus hallii*, *Senecio eleagnifolius*, and *Weinmannia racemosa*. It associates with the following lichens: *Coccocarpia erythroxyli*, *Degelia gayana*, *Erioderma chilense*, *Hypotrachyna sinuosa*, *Leioderma amphibolum*, *L. pycnophorum*; *Pannaria fulvescens*, *Physma chilense*, *Polychidium contortum*, *Pseudocyphellaria aurata*, *P. chloroleuca*, *P. episticta*, *P. faveolata*, *P. hookeri*, *P. intricata*, *P. multifida*, *P. rufovirescens*, *Sticta latifrons*, and *S. caliginosa*.

Specimens examined: 14 [see also Renner & Galloway (1982)].

39. **Pseudocyphellaria neglecta** (Müll. Arg.) Magnusson **Fig. 104**

in *Acta Horti gothoburg.* **14**: 30 (1940). – *Stictina neglecta* Müll. Arg. in *Flora, Jena* **70**: 58 (1887). – *Sticta neglecta* (Mull. Arg.) Zahlbr., *Cat. Lich. Univ.* **3**: 396 (1925). Type: Australia, New England, sine collectoribus nomine (G 002121! – holotype).

Stictina crocata f. esorediosa Müll. Arg. in *Flora, Jena* **66**: 354 (1883). – *Pseudocyphellaria crocata* var. *esorediosa* (Müll. Arg.) Vainio, *Résult. Voy. S. Y. Belgica, Bot. Lich.*: 29 (1903). Type: Australia, Mount Napier, Victoria. '*Sidney: Johnson*', ex F. v. Mueller 1883 (G! – lectotype).

Stictina mougeotiana var. *dissecta* Müll. Arg. in *Bull. Soc. Bot. Belg.* **31**: 27 (1892). *Pseudocyphellaria mougeotiana* var. *dissecta* (Müll. Arg.) Vainio in *Hedwigia* **37**: 34 (1898). – *Sticta mougeotiana* var. *dissecta* (Müll. Arg.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 33 (1896). Type: New Zealand, sine loco (prob. Wellington), *C. Knight* (G 002247! – holotype).

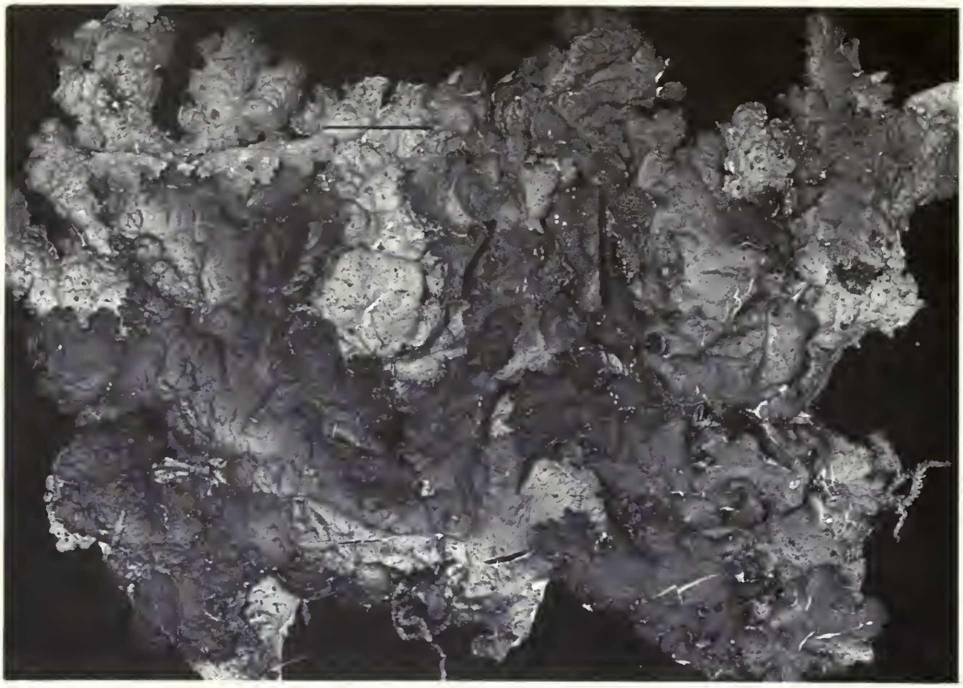

Fig. 104 *Pseudocyphellaria neglecta*. Port Hills, *Allan* (CHR 374772). Scale = 2 cm.

Pseudocyphellaria australiensis Magnusson in *Acta Horti gothoburg*. **14**:9 (1940) Fig. 1. Type: Australia, South Australia, Encounter Bay, *W. Cleland* 1926 (UPS! – holotype).

Morphology: *Thallus* orbicular to spreading, rather irregular, 3–12(–20) cm diam., loosely attached centrally, margins free, saxicolous, terricolous, corticolous. *Lobes* very variable 0·2–2·5 cm wide, short, linear-laciniate to broadly rounded, discrete to imbricate, concave to plane. *Margins* entire, incised, crenate dentate, often densely phyllidiate, sinuous, ascending towards apices, slightly thickened below, occasionally with minute, puncate, yellow, pseudocyphellae. *Upper surface* dark leaden-grey or blue-grey suffused red-brown or fawnish in parts when moist, olivaceous-brown, red-brown, brownish yellow to glaucous-brown or reddish to ± blackened in exposed habitats when dry, ± wrinkled to faveolate, interconnecting ridges rather low, rounded, faveolae shallow, flaccid when wet, rigid, brittle when dry, smooth, somewhat coriaceous, without soredia, isidia, maculae or pseudo-cyphellae, occasionally wrinkled, ridged, marginal and laminal phyllidia may erode and expose yellow medulla. *Phyllidia* mainly marginal, rarely laminal on ridges and/or breaks in thallus, simple to ± coralloid, 0·05–0·1 mm tall. *Medulla* yellow. *Photobiont Nostoc*. *Lower surface* pale buff to chestnut-brown at margins, black centrally, glabrous in a narrow marginal band, or tomentose from margins to centre, wrinkled, occasionally ± bullate, tomentum short, velvety, whitish to grey-brown. *Pseudocyphellae* yellow, scattered, sparse to frequent, 0·1–0·3(–0·5) mm diam., round to irregular, flat or shallowly verruciform, plane or slightly sunk in tomentum. *Apothecia* sparse to common, mainly marginal and occasionally also laminal, rounded, subpedicellate, 0·5–3·5 mm diam., markedly concave to plane, disc dark red-brown to black, smooth, matt, epruinose, margins pale, smooth to crenate, dentate or scabrid, exciple pale flesh-coloured to red-brown, translucent when moist, corrugate-scabrid, tomentose towards base.

Anatomy: Thallus 230–360 μm thick. *Upper cortex* 56–73 μm thick, upper 12 μm densely compacted cells scarcely apparent, appearing as ± transparent gel, cells colourless, 1·5–7 μm diam. *Photobiont Layer* 45–56 μm thick, in irregular clumps intersected by loosely interwoven strands of red-brown hyphae, *photobiont Nostoc*. *Medulla* 90–185 μm thick, pale straw-yellow,

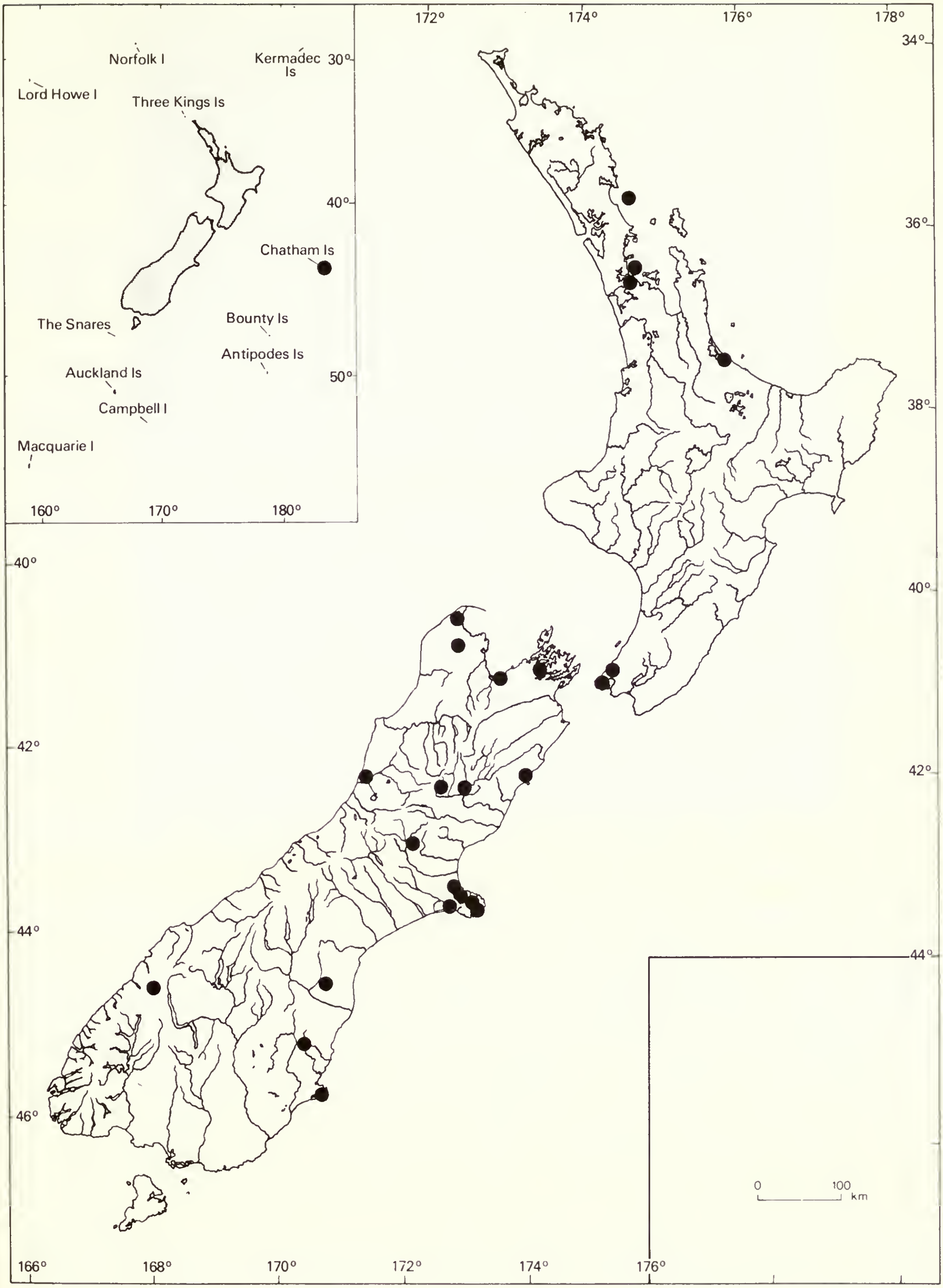
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Fig. 105 Distribution of *Pseudocyphellaria neglecta*.

hyphae encrusted with white granular crystals. *Lower cortex* 18–27 μm thick, outermost cells dark red-brown, inner cells pale yellow-brown, 6·5–15·5 μm diam. *Tomental hairs* red-brown encrusted with crystals, to 5 μm diam., 45–140(–270) μm long. *Apothecia: Exciple* colourless to pale yellow-brown in outer parts, 80–140 μm thick, cells 4·5–14 μm diam. *Hypothecium* 67–75 μm thick, pale yellow-brown, dissolving in K. *Thecium* 72–80 μm tall, pale straw-yellow; *epithecium* pale to dark yellow- or olive-brown, 7–9 μm thick, dissolving in K. *Asci* 57–68 × 13·5–15 μm. *Ascospores* yellow-brown to dark red-brown, thickened 1-septate to 3-septate, locules irregular, broadly ellipsoid to oval-ellipsoid 20.5–25 × 7–9 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, tenuiorin, methyl gyrophorate, gyrophoric acid (tr.), physciosporin (rare), methyl virensate (rare), hopane-6α, 7β, 22-triol, norstictic, stictic, crypotostictic, and constictic acids. In about one fifth of the specimens examined, stictic acid and its associated metabolites are replaced by salazinic and consalazinic acids.

Distinguishing features: *Pseudocyphellaria neglecta* is an Australasian or possibly palaeotropical species having linear-laciniate to broadly rounded lobes with entire to crenate-incised, often densely phyllidiate margins. The upper surface is ± wrinkled to faveolate, occasionally with phyllidia regenerating from cracks. It has a white medulla, a blue-green photobiont, and a pale buff to brown or ± blackened tomentose lower surface, with scattered yellow pseudocyphellae. Apothecia are sparse to frequent, subpedicellate with a conspicuous, corrugate-scabrid pale pinkish to red-brown exciple. Spores yellow-brown to dark red-brown, thickened 1-septate to 3-septate. It has a complex chemistry containing pigments, depsides, depsidones (including the rather rare compound physciosporin), and hopane-6α, 7β, 22-triol. In some specimens (*c.* 20% stictic acid and its metabolites are replaced by salazinic acid (Galloway *et al.*, 1983*b*).

Variation: *Pseudocyphellaria neglecta* has a rather uniform morphology in New Zealand but is more polymorphic in Australia, and does not show the wide morphological variation of the related species *P. crocata*. The two species have an identical chemistry (see under *P. crocata*), even to the extent of the replacement of stictic acid metabolites by salazinic acid in *c.* 20% of specimens examined. However, *P. neglecta* differs from *P. crocata* in the absence of soredia, the marginal phyllidia (which may sometimes be eroded apically and appear pseudosorediate), and the often copious development of apothecia. It also tends to be a rather more robust and larger plant than *P. crocata*, preferring drier habitats, which may account for the more uniform morphology. The tropical species *P. desfontainii* differs from *P. neglecta* in having scattered, laminal, finger-like isidia, and lacking both phyllidia and soredia.

Distribution: (Fig. 105) Widespread but still rather poorly collected in New Zealand. From Hen I., lat. 36°S) to the Otago Peninsula, coastal to subalpine, sea-level to 1000 m.

Habitat ecology: *Pseudocyphellaria neglecta* occurs on rocks in grassland (it is common in such habitats on Banks Peninsula), on soil, on coastal rock faces, on dead *Nothofagus* stumps, and on scrub in subalpine areas. It is an epiphyte of twigs and branches of *Leptospermum scoparium* and *Metrosideros excelsa*. It occurs most commonly in drier, eastern South I., habitats, especially those exposed to full sunlight. It is still much in need of collection and study in New Zealand.

Specimens examined: 30. [Josephine Tilden's South Pacific Plants. 157 sub *Sticta crocata*, from Epsom, Auckland, collected in 1909 is referable to *P. neglecta*].

40. Pseudocyphellaria nermula D. Galloway, **sp. nov.** **Fig. 106**

Diagnosis: *Pseudocyphellariae ardesiacae* similis sed thallus supra phyllidiatus, sorediis destitutus. Typus: New Zealand, South I., Canterbury, Boyle River, on bark of *Nothofagus solandri* var. *cliffortioides*, 29 March 1980, *D. J. Galloway* (CHR 379996! – holotype; BM ! – isotype). [t.l.c.: pulvinic acid, pulvinic dilactone, calycin, and a mixture of stictane triterpenoids similar to those found in *P. ardesiaca*.]

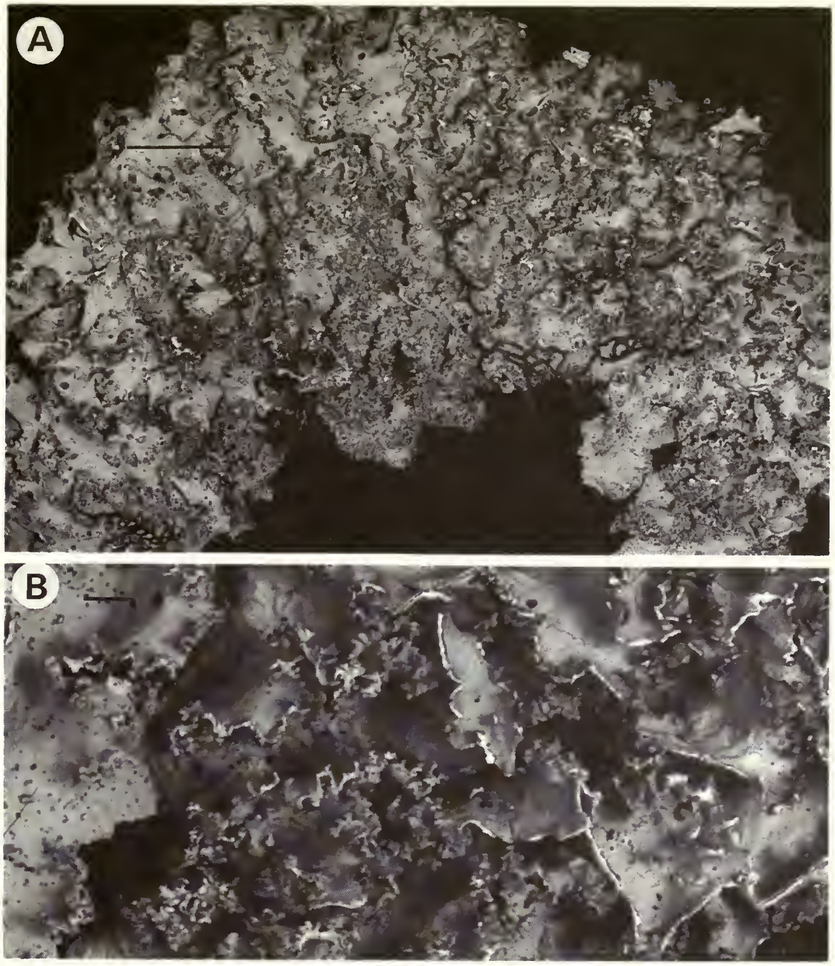

Fig. 106 *Pseudocyphellaria nermula*. Holotype (CHR). A. Scale = 1 cm. B. Scale = 1 mm.

Morphology: *Thallus* rosette-forming, 2–5(10) cm diam., loosely attached over whole of lower surface, margins somewhat ascending, corticolous (muscicolous). *Lobes* complex-imbricate, 5–10(–12) mm wide, convex to plane, not easily distinguished, ± coalescing centrally, margins crenate-dentate and complexly sinuous at lobe apices, becoming densely phyllidiate centrally, not sorediate or pseudocyphellate, strongly thickened and slightly inflexed below. *Upper surface* pale grey-blue to dark slate-blue when wet, pale greyish buff with a slight pale bluish or olivaceous tinge when dry, algal-free areas pale whitish buff, margins of lobes and phyllidia suffused brown to red-brown to ± blackened, shallowly and minutely wrinkled-uneven, ± pitted in places, often minutely areolate-scabrid(× 10 lens), rarely patchily tomentose near lobe apices, tomentum short, velvety, white or buff, matt, rather coriaceous, shining in parts, without isidia, soredia or pseudocyphellae. *Phyllidia* primarily marginal, flattened, dorsiventral, lower surface pale yellow, corticate, without pseudocyphellae, upper surface concolorous with thallus or somewhat darkened brownish to blackened, developing from crenulate margins, occasionally also on laminal ridges, 0·1–0·4 mm tall and to 0·4 mm wide, clustered, simple, tear-shaped at first, soon becoming nodular-glomerulate to ± coralloid-branched. *Medulla* yellow. *Photobiont Nostoc*. *Lower surface* pale yellow or buff, ± uniformly tomentose from margins to centre, tomentum thin, velvety at margins, thicker and more woolly towards centre, very evenly and rather densely and tightly developed, whitish or yellow-buff at

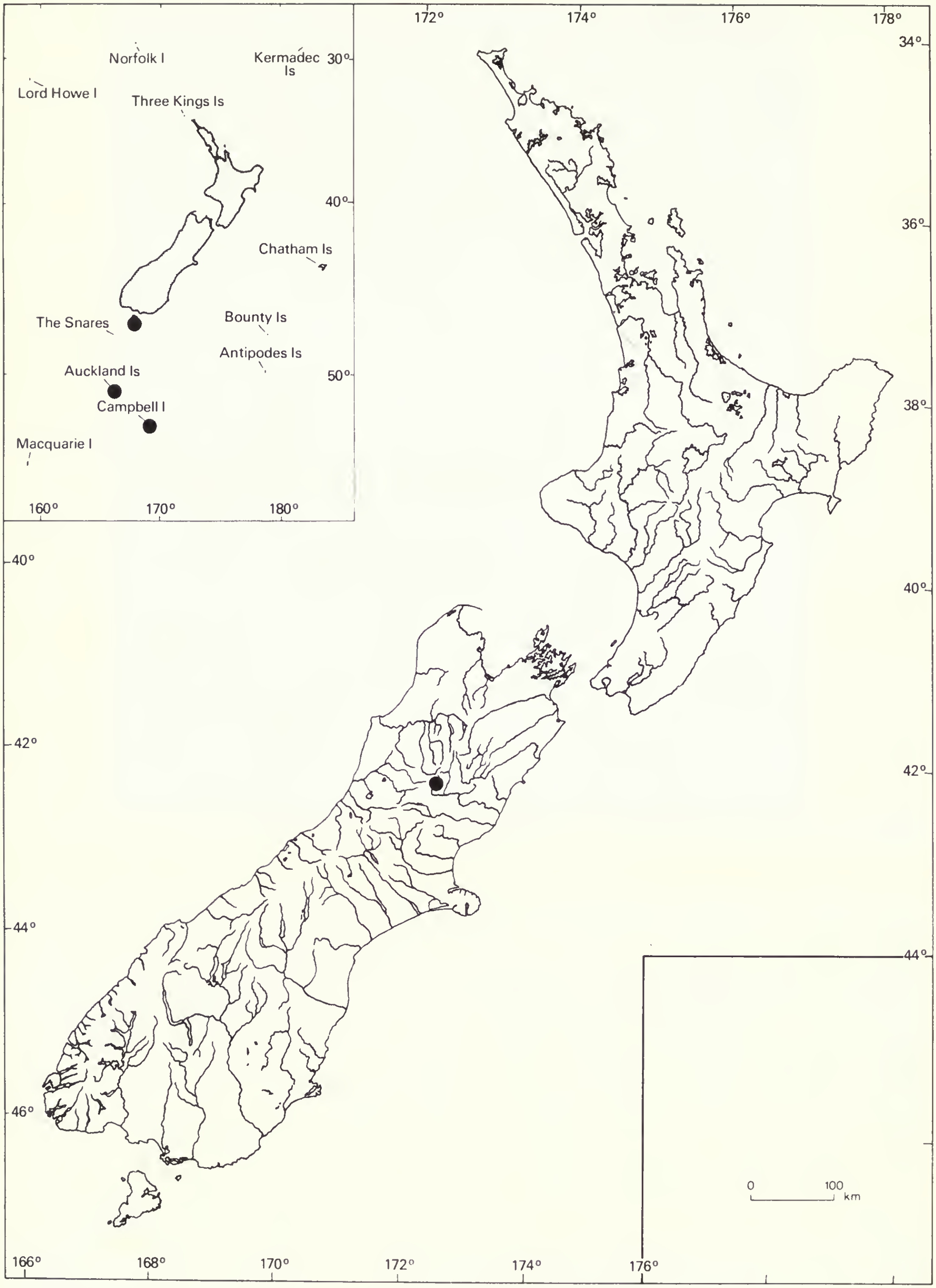
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Fig. 107 Distribution of *Pseudocyphellaria nermula*, and *P. physciospora* (inset).

margins, red-brown centrally. *Pseudocyphellae* sparse, scattered, yellow, pulverulent, convex, conspicuously projecting above tomentum, 0·2–0·5 mm diam., rather rare at margins, more common and prominent centrally. *Apothecia* and *pycnidia* not seen.

Anatomy: *Thallus* 180–275(–320) μm thick. *Upper cortex* 36–44(–55) μm thick, outermost layer roughened-uneven, upper 18-22 μm dilute yellow-brown, cells rather small and compressed, remainder of tissue colourless, a somewhat loose, anticlinally arranged pseudoparenchyma of thin-walled, round to irregular cells 4·5–13·5 μm diam., cells near photobiont layer largest. *Photobiont layer* 80–100 μm thick, yellow-brown in upper part, greenish below, densely compacted, *photobiont* blue-green, *Nostoc*, in coiled chains, in clusters surrounded by a colourless, gelatinous envelope, cells round, 5–9 μm diam. *Medulla* 64–100(–165) μm, loosely interwoven to ± compact, hyphae pericilinally arranged, to 4·5 μm diam., encrusted with granular, yellow crystals. *Lower cortex* 22–33 μm thick, pale straw-coloured of 6–7 rows of round to irregular thick-walled cells, 4·5–13·5 μm diam., walls 2–2·5 μm thick, lumina round to rectangular 2·5–9 μm diam. *Tomental hairs* colourless, septate, cells short constricted at septa, ± moniliform, to 7 μm diam., and 45–140(–185) μm long, in clustered fascicles, mainly simple, 2–3-branched at apices.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin and a mixture of stictane triteprenoids similar to those found in *P. ardesiaca*.

Distinguishing features: *Pseudocyphellaria nermula* is a distinctive, rosette-forming, endemic species having a yellow medulla, a blue-green photobiont, and characteristic marginal (rarely laminal), simple to coralloid-branched phyllidia. The upper surface is also ± minutely scabrid-areolate (× 10 lens). It has a complex chemistry similar to that of *P. ardesiaca*. It is not known fertile.

Variation: This species is known only from the type locality, and the two extant collections are not sufficient to allow speculation on the morphological variation shown by the species. *Pseudocyphellaria nermula* is one of three small, rosette-forming, yellow-medulla, blue-green photobiont species found in primarily subalpine areas of South I. The presence of marginal phyllidia distinguishes *P. nermula* from the related *P. ardesiaca* which is sorediate, and from *P. jamesii* which has rather narrower lobes which are ± subdichotomously branched and also weakly to strongly reticulate-faveolate but which lack soredia and phyllidia. *Pseudocyphellaria nermula* (which is named for my wife) resembles some forms of *P. pickeringii* but is distinguished from this species by the blue-green photobiont.

Habitat ecology: The type collection was made from the bark of mountain beech (*Nothofagus solandri* var. *cliffortioides*) in semi-open forest on the banks of the Boyle River (172°23′E: 42°31′S, at 585 m alt.). The species forms characteristic rosettes amongst mosses and other lichens including: *Pseudocyphellaria gretae*, *P. pickeringii*, *P. pubescens*, *Sphaerophorus tener*, and *Usnea capillacea*.

Specimens examined: (Fig. 107) South Island. Canterbury: Boyle River near Lewis Pass, 29 March 1980, *D. J. Galloway* (CHR 379996, BM).

41. **Pseudocyphellaria physciospora** (Nyl.) Malme **Fig. 108**

in *Bih. K. svenska Vetensk.-Akad. Handl.* **25** (3/6): 20 (1899). – *Sticta fossulata* subsp. *physciospora* Nyl., *Syn. meth. lich.* **1** (2): 364 (1860). – *S. physciospora* (Nyl.) Nyl. in *J. Linn. Soc. Lond.* (Bot.) **9**: 248 (1866). – *Phaeosticta physciospora* (Nyl.) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Lobaria physciospora* (Nyl.) Hellbom in *Bih. K. svenska Vetensk.-Akad. Handl.* **21** (3/13): 38 (1896). – *Diphaeosticta physciospora* (Nyl.) Clements, *Gen. fung.*: 175 (1909). Type: Auckland [Island], *Hombron* (PC-HUE! – lectotype) [see note 1].

Sticta cellulifera sensu J. D. Hook., in Taylor & J. D. Hook., *Fl. antarct.* **I**: 198 (1845) [see note 2].

Note 1: *Sticta fossulata* subsp. *physciospora* Nyl.

The lectotype specimen of *S. fossulata* subsp. *physciospora* is on a sheet in PC-HUE [recently found by Prof. Hannes Hertel, Munich] together with three other specimens, two being referable to *Pseudocyphel-*

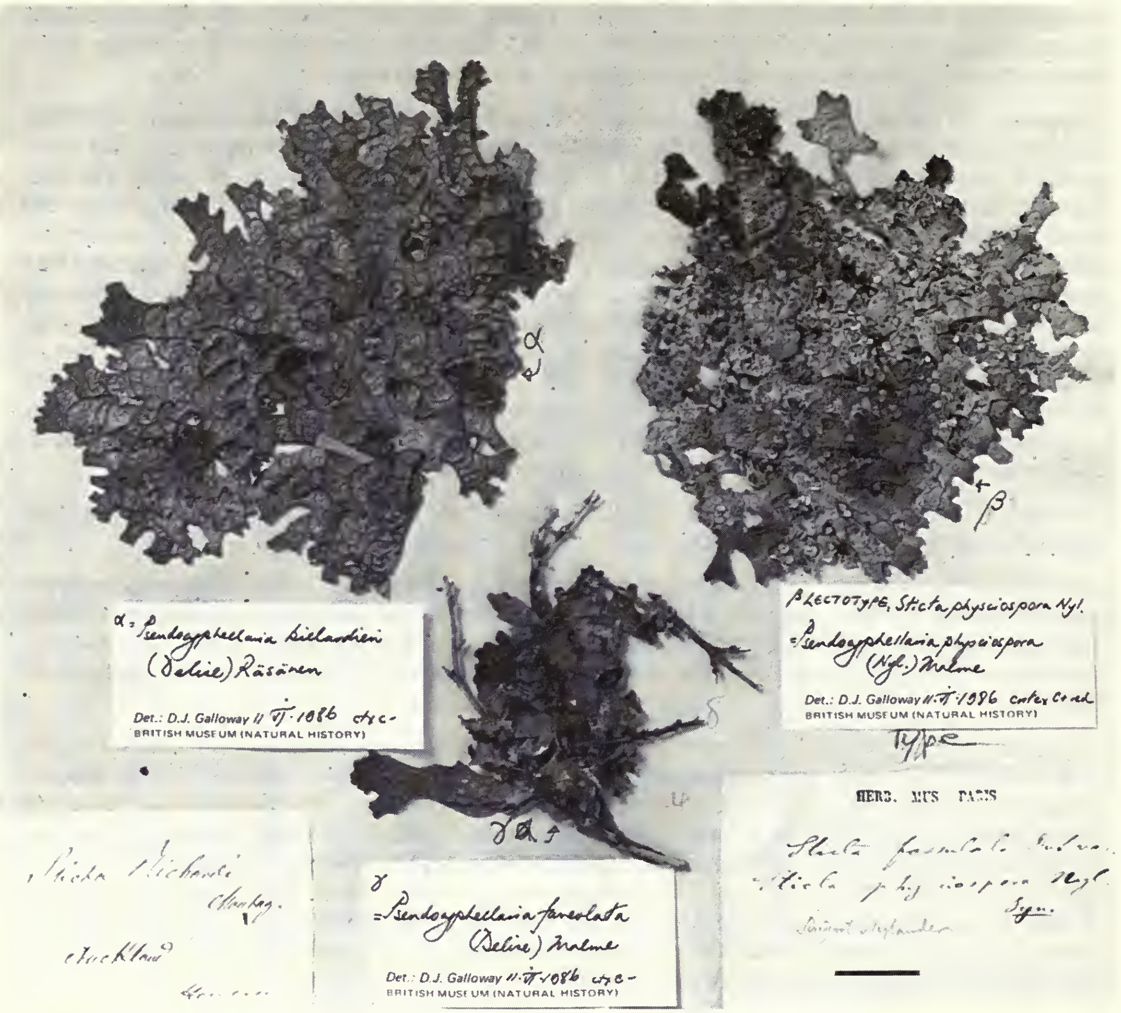

α
α = Pseudocyphellaria billardierei (Delise) Räsänen
Det.: D.J. Galloway 11 VI 1986
BRITISH MUSEUM (NATURAL HISTORY)
β
β LECTOTYPE, Sticta physciospora Nyl.
= Pseudocyphellaria physciospora (Nyl.) Malme
Det.: D.J. Galloway 11.VI.1986
BRITISH MUSEUM (NATURAL HISTORY)
Type
HERB. MUS. PARIS
Sticta fossulata Duf. var.
Sticta physciospora Nyl.
Syn.
Sticta Richardi
Montag.
Auckland
γ
γ = Pseudocyphellaria faveolata (Delise) Malme
Det.: D.J. Galloway 11.VI.1986
BRITISH MUSEUM (NATURAL HISTORY)

Fig. 108 *Pseudocyphellaria physciospora*. Lectotype of *Sticta physciospora* (PC-HUE). Scale = 2 cm.

laria billardierei, and one to *P. faveolata* (Fig. 108). The sheet has two labels: that at the left-hand corner is in Montagne's hand and states 'Sticta Richardi Montag. Auckland. Hombron', while that at the right-hand corner is in Nylander's hand and states 'Sticta fossulata Duf. var. Sticta physciospora Nyl. Syn.'. The Auckland referred to in Montagne's label is the Auckland Islands south of New Zealand, and not the town or province of Auckland in North I. Montagne refers to Hombron's collections of *S. richardi* thus 'ad rupes truncosque arborum vetustos montium in insulis Auckland et Akaroa Novae-Zeelandiae' (Montagne, 1845: 187). Montagne's use of *S. richardi* in New Zealand thus refers to the taxa *Pseudocyphellaria billardierei*, *P. physciospora*, and also to *P. rufovirescens* (see under this species).

When proposing the name *physciospora* as a subspecies of *Sticta fossulata* [= *P. billardierei*] Nylander noted the very close similarity of the two taxa, basing the subspecies on the brown *Physcia*-like spores, and on the yellow or yellowish pseudocyphellae, 'cyphellis saepius albo-flavescentibus vel subcirtinis (rarius albis)' (Nylander, 1860*b*: 364). Nylander later raised his subspecies to specific rank as *Sticta physciospora* (Nylander, 1866, 1888*b*), but also referred to it as a variety of *S. fossulata* (Nylander, 1868*b*). As Lindsay (1869: 501) correctly noted 'The character on which Nylander apparently founds his species – the polari-bilocular or physcioid spores – is not a constant or distinctive one, inasmuch as, we have already seen, it occurs in various forms of *S. fossulata*; and we shall hereafter find it occurs also in other *Stictæ*'.

However, Nylander's initial observations on the yellow pseudocyphellae and the subdenticulate apothecial exciple in specimens from the Auckland Is are useful in helping separate *P. physciospora* from related taxa, a segregation reinforced by reactions of epithecial pigments (Hue, 1890; Imshaug, 1977), chemistry, and morphology. Later accounts of *P. physciospora* (Hue, 1890; Stizenberger, 1895; Malme, 1899) mention the thickened epispore and the narrow channel separating the two locules of the 'physcioid' spore, and the yellowish pseudocyphellae as major differentiating characters. Hue (1890: 46) gives a full description of the species [although it appears to be based on mixed collections of both *P. physciospora* and *P. faveolata*], and mentions the K+ violet epithecial reaction. Nylander (1866, 1888) seems to have confused *P. physciospora* with *P. faveolata* and several specimens annotated by him as *P. physciospora* (BM, PC-HUE) are *P. faveolata*, a fact which led Galloway & James (1980) and Galloway (1985*b*) to make *P. physciospora* a synonym of *P. faveolata*. A specimens of *P. carpoloma* in Charles Knight's herbarium (WELT) is annotated by Nylander 'Sticta physciospora Nyl. Syn. p. 364 (f. cyphellis citrinis)'.

Imshaug (1977) gives the first correct modern circumscription of *P. physciospora*, and highlights the distinctive chemistry of this species which contains appreciable quantities of norstictic and salazinic acids (both rather rare in any quantity in species of *Pseudocyphellaria* in New Zealand), has tenuiorin and methyl gyrophorate as principal depsides, and which lacks physciosporin, the characteristic marker depsidone of *P. faveolata*.

Note 2: *Sticta cellulifera* sensu J. D. Hook.
Hooker's account of *S. cellulifera* (Taylor & Hooker, 1845: 198) from the Auckland Is and Campbell I., differs from the type description of *S. cellulifera* which is a synonym of *P. faveolata*. All of the material seen labelled *Sticta cellulifera* by Thomas Taylor (BM, FH) contains physciosporin, has white pseudocyphellae on the lower surface and along the margins of the lobes, and has occasionally white-pruinose apothecial discs, all characters of *P. faveolata*. On the other hand, material collected by Hooker from the Auckland and Campbell Is, with yellow pseudocyphellae must refer to *P. physciospora*, and his notes on the collections (p. 198) very strongly suggest this, 'We know of no single character by which this form, which is as variable as any of its congeners, may be recognised. In its normal state the whole frond is fully a span across, all parts of it rugose with deep lacunae; specimens from the woods are of a lax habit, with lobes an inch broad, of a pale brown or yellow beneath; those from the mountains, again, are deep olive green and almost black beneath, with the lobes short and round, and the cyphellae of a bright yellow. In many respects it is very closely allied to the *S. carpoloma*, Delise, which, according to Montagne (whose authentically named collection of *Stictæ* is the completest I have seen), has the apothecia invariably marginal. The present plant includes in part both *S. impressa* and *S. cellulifera*, of the 'London Journal of Botany'.'

Morphology: Thallus rosette forming to irregularly spreading, 5–15 cm diam., closely to loosely attached centrally, margins ± free, corticolous. *Lobes* divergent, di- or trichotomously branched, rather broad, 5–10(–20) mm wide, discrete and ± truncate at apices, ± imbricate centrally, sinuses circular. *Margins* entire, rounded, distinctly ridged above, without projecting pseudocyphellae, noticeably thickened below. *Upper surface* olive-green to yellow-green when moist, often suffused red-brown towards lobe apices, olivaceous, brownish when dry, strongly to weakly reticulate-faveolate, interconnecting ridges prominent, broad, rather flat, matt or shining, without soredia, isidia, phyllidia, maculae, papillae or pseudocyphellae. *Medulla* white. *Photobiont* green. *Lower surface* glabrous and shining in a broad to narrow marginal zone, tomentose centrally, occasionally to margins, tomentum short, velvety-pubescent, white or buff, smooth to wrinkled or puckered at margins, ridged-bullate centrally. *Pseudocyphellae* yellow, rather inconspicuous, sparse to numerous, widely scattered, raised, verruciform, 0·1 mm diam. or less, rarely to 0·2 mm, decorticate area flat, pin-prick-like. *Apothecia* sessile to ± pedicellate at maturity, marginal and laminal, rounded, 0·5–4(–5) mm diam., deeply cupuliform at first, becoming shallowly concave at maturity, disc dark red-brown to black, shining, epruinose, smooth, margins scabrid-areolate, pale flesh to red-brown, conspicuously dentate-stellate in old fruits, exciple pale flesh to red-brown at margins of disc, coarsely corrugate or scabrid-areolate. *Pycnidia* common to rare, scattered laminally, mainly on thallus ridges, black, minute, 0·1 mm diam. or less, punctate-impressed.

Anatomy: Thallus 180–350(–550) µm thick. *Upper cortex* (25–)30–40 µm thick, pale straw-yellow in upper parts, remainder colourless, outermost cells compressed, cells 2–4·5 µm diam. *Photobiont layer* 90–110 µm, *photobiont* green, cells rounded, to 9 µm diam. *Medulla* 250–450 µm thick, colourless. *Lower cortex* 20–35 µm thick, pale straw-yellow to dilute brownish, of 4–6 rows of cells. *Tomental hairs* in fascicles, 55–120 µm long, colourless, cells 5–7 µm thick.

Apothecia: Exciple exterior to a narrow photobiont layer and a thicker medulla supporting the thecial layers, colourless, 55–90 μm thick, pale straw-yellow in outer parts, hyaline internally, in discrete, pyramidal groups at exterior, cells small, 3–5 μm diam. *Hypothecium* pale yellow-brown, 30–45 μm thick, unchanged in K. *Thecium* colourless or pale straw-yellow, 75–90 μm tall; *epithecium* dark red-brown, 4–7 μm thick, violet-purple in K. *Asci* 75–85 × 15–18 μm. *Ascospores* brown, mainly 1-septate, fusiform to oval-ellipsoid, (21–)23–29(–32) × 7–9 μm.

Chemistry: Methyl evernate, tenuiorin, methyl gyrophorate, gyrophoric acid, 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol, hopane-6α, 7β, 22-triol, two unidentified triterpenoids, norstictic, salazinic, consalazinic, stictic, cryptostictic, connorestictic, and constictic acids, three unidentified depsidones, pulvinic dilactone (tr.), and calycin (tr.).

Distinguishing features: Pseudocyphellaria physciospora is an austral species characterized by broad, rather divergent lobes, di-or trichotomously branched, with entire margins, thickened above and below, but lacking pseudocyphellae. The upper surface is matt, reticulate-faveolate, without isidia, maculae, phyllidia, pseudocyphellae, or soredia. It has a white medulla, a green photobiont, and a pale buff of whitish, velvety, short-tomentose lower surface with a prominent, glabrous marginal zone, and with minute, inconspicuous, yellow pseudocyphellae. Apothecia are marginal and laminal, ± pedicellate, the disc dark red-brown, shining, epruinose, the exciple pale to red-brown, coarsely corrugate to dentate-stellate (Fig. 109). Epithecium dark red-brown, turning violet-purple in K. Spores brown, thickened, 1-septate to 3-septate. It has a complex chemistry containing several hopane triterpenoids, tenuiorin, norstictic, and salazinic acid, and traces of the pigments calycin and pulvinic dilactone present in the pseudocyphellae.

Variation: The relatively small number of specimens examined (20) all seemed morphologically quite uniform and all have rather broad lobes which have entire, thickened margins without projecting pseudocyphellae, a character which distinguishes *P. physciospora* from *P. faveolata* and *P. carpoloma* (Table 2). It differs from *P. faveolata* also in chemistry and in the non-pruinose apothecial discs; from *P. rufovirescens* in epithecial pigments, yellow pseudocyphellae, chemistry, and a tomentose lower surface; from *P. billardierei* in the yellow pseudocyphellae, differing epithecium reactions in K, and a different chemistry. The northern species, *P.*

Table 2 Faveolate species of *Pseudocyphellaria* with a green photobiont.

Character	*billardierei*	*carpoloma*	*durietzii*	*faveolata*	*physciospora*	*rufovirescens*
Spores thickened, 1-septate	+	+	+	+	+	−
Epithecium K + green-black	+	−	−	−	−	−
Epithecium K + rose-purple	−	−	+	+	+	−
Pseudocyphellae at margins	−	+	−	+	−	−
Pseudocyphellae yellow	−	+	−	−	+	−
Apothecial disc pruinose	−	−	−	+	−	−
Methyl evernate	+	+	+	−	+	−
Tenuiorin	+	+	+	−	+	−
Methyl lecanorate	+	+	+	−	+	−
Methyl gyrophorate	+	+	−	−	+	−
Gyrophoric acid	+	tr	+	−	−	−
7β-acetoxyhopan-22-ol	−	−	−	−	+	+
Hopane-7β, 22-diol	−	+	+	tr	+	tr
Hopane-15α, 22-diol	−	−	−	−	−	+
Hopane-6α, 7β, 22-triol	−	+	+	+	+	−
Zeorin	+	−	−	−	−	−
Methyl virensate and physciosporin	−	−	−	+	−	−
Norstictic acid	tr	−	tr	−	+	−
Salazinic acid	−	−	−	−	+	−
Stictic acid complex	+	+	+	+	+	−

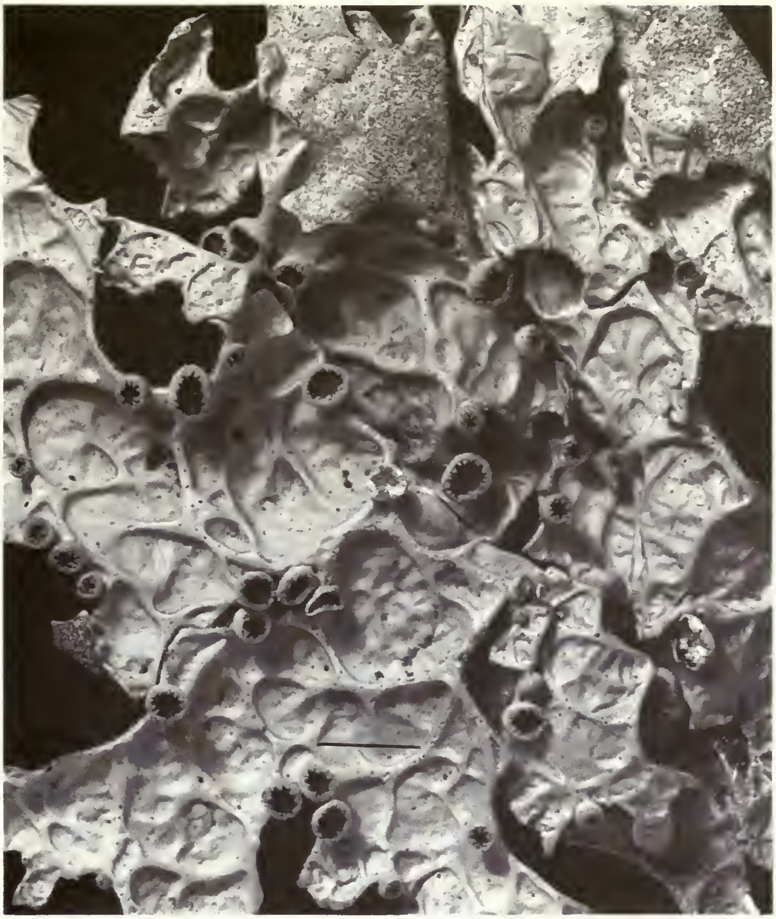


Fig. 109 *Pseudocyphellaria physciospora*. Ranui Cove, Auckland Island, *Meurk* (CHR 343127). Scale = 5 mm.

carpoloma, is similar but has narrower lobes, with prominent pseudocyphellae at the lobe margins and on the lower surface, and it lacks salazinic acid.

Distribution: (Fig. 107) Known from the subantarctic Auckland and Campbell Is, and from Stewart I., sea-level to 500 m. Also from Juan Fernandez.

Habitat ecology: *Pseudocyphellaria physciospora* is an epiphyte of coastal scrub (also coastal forest trees in the Auckland Is) and of subalpine scrub associations in tussock grassland in inland sites. It is most commonly collected from *Coprosma ciliata*, *Dracophyllum longifolium*, *Metrosideros umbellata*, *Metrosideros umbellata*, *Myrsine divaricata*, *Pseudoparax simplex*, and *Senecio reinoldii*, where it associates with other species of *Pseudocyphellara* viz., *P. billardierei*, *P. coronata*, *P. faveolata*, *P. glabra*, *P. multifida*, and *P. rubella.*

Specimens examined: Stewart Island. Tommy Island (Bravo Group), 19 March 1980, *C. D. Meurk* (BM, CHR). Auckland Island: Ranui Cove, 2 April 1980, 2, 14 April 1980, *C. D. Meurk* (BM, CHR); between Smith Harbour and Norman Inlet, 1 January 1973, *H. A. Imshaug* 37256 (MSC); head of North Harbour, 12 January 1973, *H. A. Imshaug* 57773, 57771 (MSC). Enderby Island: NNE of Sandy Bay, 13 December 1972, *H. A. Imshaug* 56342 (MSC); Sine loco, Admiral *D'Urville* (PC-MONTAGNE); Campbell Island: Cliffs between Mt Azimuth and Couvrejolles Peninsula, 30 December 1969, *H. A. Imshaug* 46320 (MSC); Lyell Ridge, 23 December 1969, *R. C. Harris* 4426 (MSC); 24 December 1969, *H. A. Imshaug* 46083 (MSC);

NW of Sorensen Hut, 18 January 1970, *H. A. Imsahug* 47212, 47215, 47237 (MSC); between Penguin Bay and Menhir Peak, 28 December 1969, *R. C. Harris* 4709 (MSC); NE of Mt Sorensen, 6 January, 1970, *R. C. Harris* 5117 (MSC); E. slope of Paris-Villarceau Ridge, 5 January 1970, *H. A. Imshaug* 46615 (MSC); between Garden Cove and Filhol-Honey Saddle, 23 December 1969, *H. A. Imshaug* 46093 (MSC); N. slope of Filhol Peak, 19 January 1970, *R. C. Harris* 5573 (MSC); Mt Beeman, 4 April 1959, *sine collectoribus* (BM ex OTA).

42. **Pseudocyphellaria pickeringii** (Tuck.) D. Galloway, **comb. nov.** **Figs 110, 111**

Sticta pickeringii Tuck. in *U.S. Exploring Exped.* **17** (Bot.): 138 (pl. 1, fig. VI, 1 & 2) (1874). Type: New Zealand, Bay of Islands, Wilkes Exped., sine collectoribus nomine (FH! – holotype) [see Note 1].

Sticta durvillei sensu Church. Bab. (non Delise) in J. D. Hook., *Fl. nov.-zel.* **2**: 298 (1855) [see Note 2].

Sticta urvillei var. *flavicans* f. *laceratula* Krempelh. in *Reise Novara Bot.* **1**: 117 (1870). Type: New Zealand, sine loco, since collectorbius nomine (M – not seen).

Sticta flavissima var. *simulans* Müll. Arg. in *Bull. Herb. Boissier* **4**: 89 (1896) pr. max. p. Type: Australia, Queensland, sine loco, *F. M. Bailey* 49 (G 002011! – lectotype) [see Note 3].

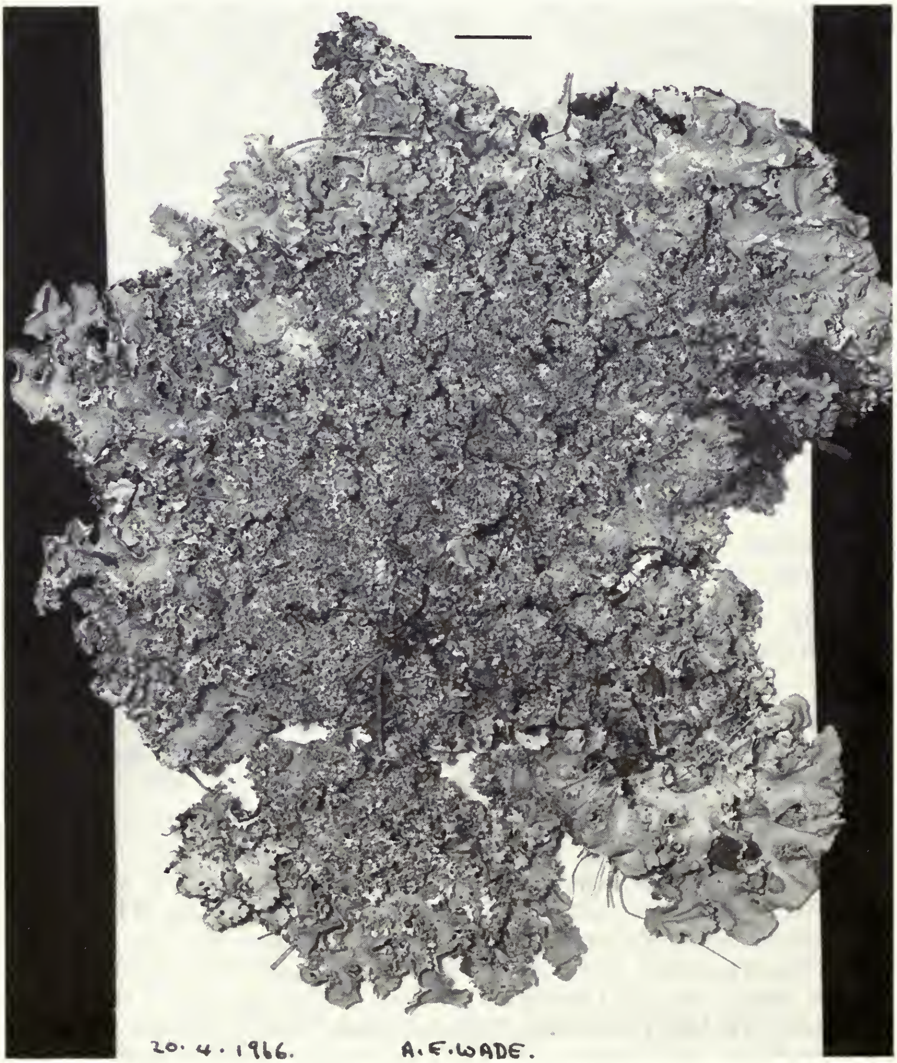


Fig. 110 *Pseudocyphellaria pickeringii*. West of Rotorua, *Wade* (BM). Scale = 1 cm.

Pseudocyphellaria flavicans auct. non (J. D. Hook. & Taylor) Vainio, see Galloway in *Fl. N.Z. Lichens*: 443 (1985) [see Note 4].

Note 1: *Sticta pickeringii* Tuck.
Tuckerman (1874: 138) qualified his type description thus 'Frond smallish, apparently somewhat rosulate, sinuate-lobate, the lobules rounded and sinuate-laciniate, and their elevated margins becoming at length thickly beset with leaflets and coralloid branchlets; glaucous-flavescent, or, at length, darker. Under side tomentose, yellowish-brown, becoming blackish at the centre. Cyphellae punctiform. Apothecia of middling size, pedicellate, the disc at length a little convex, reddish-black, the margin, and indeed the whole outside, rugulose-papillate.-Dedicated to Charles Pickering, M.D., &c., one of the Naturalists to the Expedition'.

The second United States Exploring Expedition (1838–1842), under the command of Charles Wilkes, visited the Bay of Islands in northern New Zealand in March 1840, after visiting the Antarctic, Macquarie I., and the Auckland Is (Godley, 1965). As Godley (loc. cit.) observed 'Of the three major expeditions to the Southern Ocean at this time, the American expedition like that of the French, suffered in not having a first-class botanist. This led not only to poor collecting, but to difficulties in publication. Either the participants attempted to write up the work as best they could, or the collections were studied by botanists who had not the advantage of knowing the plants in the field.' The lichens of the expedition were studied by

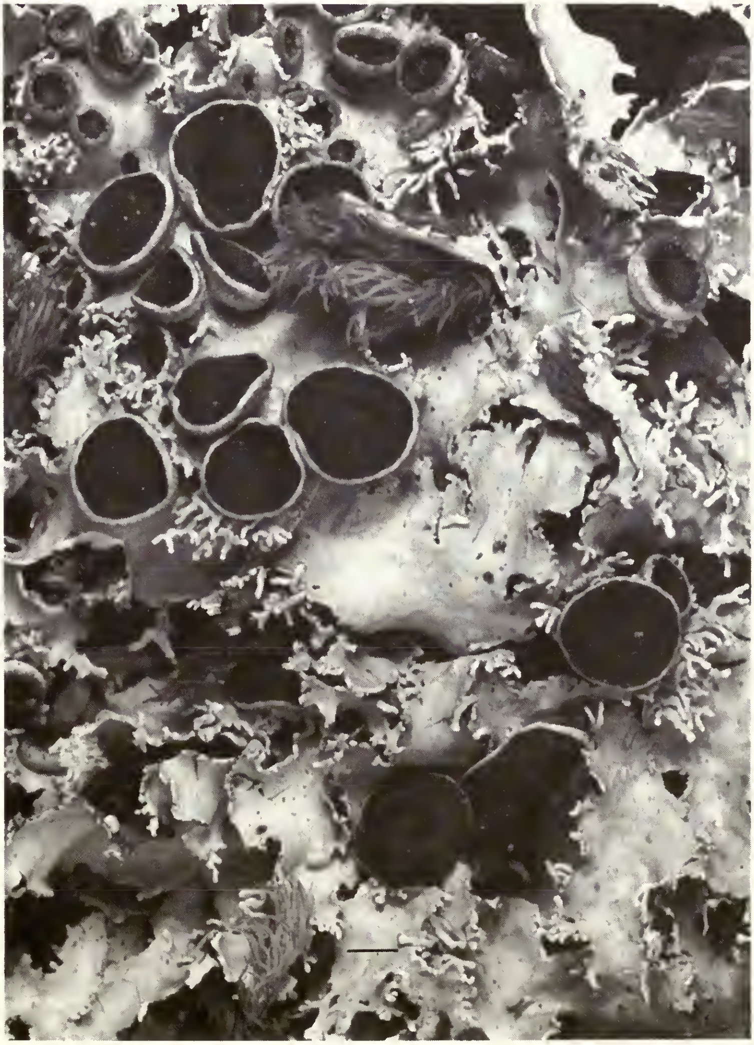


Fig. 111 *Pseudocyphellaria pickeringii*. Dog Stream, Hanmer, *Galloway* (CHR 381056) Scale = 1 mm.

Edward Tuckerman who described the present species which is a common coastal epiphyte in forests of northern New Zealand, although it has been widely known and recorded as *Pseudocyphellaria flavicans* (see note 4 below). However, Dodge (1965: 503) lectotypified *Sticta flavicans* J. D. Hook. & Taylor on material in Thomas Taylor's herbarium collected from Hermite Island, Cape Horn, which is taxonomically separable from the related species found in New Zealand. Thus the earliest available name for New Zealand material is Tuckerman's *Sticta pickeringii*.

The type of *Sticta pickeringii* has the following annotation by Tuckerman 'Sticta Zeylanica [an unpublished herbarium name] Sp. nov of Wilkes Exp. Herb. Probably what is called S. Pickeringii in the Report. The specimens were lost then, and I cd not revise my earlier work, as I wished, & Pub'd this in the faith of my origl descrn varying the name.'

The date of publication of *Sticta pickeringii* given in Zahlbruckner (1925: 344) and in Galloway & James (1980: 299) is in error, the correct date of publication of the second U.S. Exploring Expedition being 1874 (Godley, 1965).

Stizenberger (1895: 117) gives the distribution of *S. pickeringii* as 'Neuholland, Neukalidonien, Neuseeland, Nukahiwa, Sandwich Inseln, südlichtes Amerika'.

Note 2: *Sticta durvillei* sensu Church. Bab.

In his account of the New Zealand lichens, Babington (1855: 275) gives a good description of *Pseudocyphellaria pickeringii* under the name *Sticta D'Urvillei* Delise, but his description is at variance with that of Delise (1825*b*: 599) in several points, especially in detailing the isidia, structures not present in Delise's plant which is in fact *P. berberina* (see Galloway & James, 1977). Babington synonymises *Sticta endochyrsa* sensu J. D. Hook. (non Delise) with New Zealand *Sticta durvillei* adding the note 'The pulvinate coralline excrescences, the agreeable ochraceous hue, and especially the apothecia, distinguish *S. D'Urvillei* from its congeners. '*L. ochraceus*, Menzies,' [also referable to *Pseudocyphellaria berberina*] without habitat, is the name attached to specimens in Sir W. J. Hooker's herbarium, and in Aiton's (now my own) . . . Dr Hooker (with whose views Dr Montagne accords doubtfully in a MS note in Herb. Hook.) unites *S. endochrysa*, Del.! with *S. D'Urvillei*, Del.!; but the former plant has the *adult* medullary stratum almost white, whereas in *S. D'Urvillei* it is, in every stage, of a full chrome yellow; there are, besides, other differences'. Babington was correct in questioning Hooker's (1847) interpretation of *Sticta endochrysa*, an interpretation which united *Pseudocyphellaria endochrysa* sens. str. (from the Falkland Islands) with *P. berberina* (non-isidiate) and *P. flavicans* (isidiate) from Cape Horn.

Note 3: *Sticta flavissima* var. *simulans* Müll. Arg.

Lectotype material of *Sticta flavissima* var. *simulans* (G 002011) consists of one large piece (10 × 3 cm) and two fragments, all copiously isidiate and agreeing closely with the protologue. In addition, a smaller (8 × 2 cm) specimen of *Pseudocyphellaria rubrina* (Stirton) D. Galloway, is attached to the same sheet. On the type sheet of *S. flavissima* Müll. Arg. [*Flora, Jena* **66**: 21 (1883)] three fragments (*c.* 3 × 1 cm) are attached to the sheet (G 001996), the left-hand and central one being sterile, isidiate *P. pickeringii* (see Galloway 1985*a*: 306 as *P. flavicans*) and the fertile right-hand specimen being *P. rubrina*.

Note 4: *Pseudocyphellaria flavicans* auct.

Pseudocyphellaria flavicans (J. D. Hook. & Taylor) Vainio was lectotypified by Dodge (1965: 503) on material collected by Joseph Hooker from Hermite Island, Cape Horn, and predates a later and superfluous lectotypification of *Sticta flavicans* of Galloway & James (1980: 299) based on New Zealand material (BM and FH sheet 421) also collected by Hooker. This error in lectotypification was pointed out to me by Dr H. A. Imshaug who suggested that the following sentences of Dodge's constitute a valid lectotypification of *Sticta flavicans*, viz. 'In the Taylor herbarium there are six specimens published as *Sticta flavicans* Hook. f. & Taylor. The two plants from Hermite Island with small lobes, surface scrobiculate, margins sublacerate, surface partly covered by lobulate isidia in one, wholly covered in the other, the former determined as *S. D'Urvillei* Del., the latter as *S. D'Urvillei* v. *flavicans* Nyl., by Tuckerman, may be considered as the type of *Pseudocyphellaria flavicans* (Hook. f. & Taylor) Vainio' (Dodge, loc. cit.). In accordance with Art. 8.1, Dodge's treatment must be followed, and accordingly, the name *Sticta flavicans* is typified on heavily isidiate, sterile material collected from Hermite Island by Joseph Hooker.

That *Sticta flavicans* as originally described is heterogeneous and referable to several related but taxonomically distinct entities is readily seen from an examination of extant syntype material (BM, FH) bearing Taylor's annotations, a consideration of the protologue, as well as the later usage and interpretation of the name. The protologue mentions both isidia (called gemmae) and apothecia viz., 'gemmis marginalibus confertis elongatis granulatis statim explanatis . . . apotheciis stipitatis concavis extus lanuginosis disco rufo-atro margine subinegerrimis'. Taylor also added the following note to the description of *S. flavicans*, 'Nearly 1 foot wide. Towards the centre the *thallus* is sometimes rugose, but never scrobiculato-lacunose as in S. orygmaea, Ach.; besides the *soredia* are fewer, the *apothecia* receive a footstalk from the pinched up *thallus*, leaving a corresponding cavity on the inferior surface, and they are not naked exteriorly as in the Acharian species' (Hooker & Taylor, 1844: 648). Specimens seen by Taylor from which a lectotype must be selected were collected from Hermite I., Cape Horn, from the Falkland Is, and from New Zealand.

Material labelled 'Sticta flavicans Tayl.' or 'Sticta flavicans Hook. [or Hkr.] f. et Tayl.' in Taylor's handwriting is found in BM and FH (in both the Taylor and Tuckerman herbaria). The Farlow material was discussed by Dodge (1965) and consists of two collections from the Falklands [both referable to *P. endochrysa*], one of which has the name *Sticta latiloba* Tayl. crossed out and replaced by *S. flavicans* by Taylor; this specimen Dodge (loc. cit.) made the type of *P. latiloba*; two collections from Hermite I., Cape Horn-one (sheet 420) being the lectotype of *S. flavicans* (Dodge 1965: 503), and the other being *P. berberina*; three specimens from New Zealand, two of which are referable to *P. pickeringii* and one to *P. neglecta* (sheet 420). The single collection in the Tuckerman herbarium is from Cape Horn and comprises two large pieces one of which is *P. flavicans* and one *P. berberina*.

BM material annotated *Sticta flavicans* by Taylor includes (i) two collections from Hermite I.; one labelled *S. D'Urvillei* by Babington is referable to *P. berberina*, and a collection from St Martin's Cove by Mr Davis, comprising four specimens, three of which are *P. berberina* and one *P. flavicans*; (ii) one collection of J. D. Hooker from the Falkland Is, comprising mainly *P. endochrysa* with a small piece of *P. berberina*; (iii) five collections from New Zealand, one of *P. pickeringii* without a collector is annotated 'Sticta impressa Tayl.', with the epithet *impressa* struck out and *flavicans* substituted; another specimen of *P. pickeringii*, ex Herb Mus. Paris No 59, with Babington's note 'In my opinion it is a bad state of S. D'Urvillei'; a collection of Dr Stanger comprising one large piece of *P. pickeringii* and two small pieces of *P. crocata*; a specimen of *P. pickeringii* annotated by Babington 'May not this be the young of S. aurata–'; and a collection of *P. pickeringii* made by J. D. Hooker.

That Taylor included in his circumscription of *Sticta flavicans* several yellow-medulla species, both isidiate and non-isidiate, as well as both sterile and fertile material, can be seen from the description (his reference to apothecia refer to those of *P. berberina*) and from specimens examined and annotated by him. Further, letters that Taylor wrote to Hooker during their collaboration on Antarctic lichens underline his uncertainty about some of his new species of *Sticta*. Shortly after sending the manuscript on Antarctic lichens to Hooker on 2 November 1844 [*Lichenes Antarctici* . . . was published on 1 December 1844 (Sayre, 1983)] Taylor wrote again to Kew 'I have the most lively apprehensions lest some of the species I have believed to be new may turn out to be described already' (Taylor Correspondence, Royal Botanic Gardens Kew, in Director's Correspondence **103** (53), 15 November 1844). Over two years later, when Hooker was working on the publication of his *Flora Antarctica*, Taylor responded to criticism of his lichen names and especially those in *Sticta*, in the following manner, 'Your list of the errata of the Antarctic Lichens startled me but when you look over my remarks I hope you will not find things quite so bad as supposed. One kind of correction I am always prepared for and thankful for when it is made viz: the pointing out a species is previously described by some late modern author – my opportunities of consulting Continental works very seldom occur . . . S. flavicans H. Fil. & T. – if you have compared it, of course it may be 'S. endochrysa also S. D'Urvillei and S. ochracea'. I have never seen authentic specimens of the last three; by whom are they respectively described?' (Taylor Correspondence, Royal Botanic Gardens, Kew, in Director's Correspondence **103** (90), 23 April 1847).

New Zealand material referable to *P. pickeringii* was recorded under a variety of names in the 19th century literature: *Sticta flavicans* (Hooker & Taylor, 1844; Raoul, 1846; Lindsay, 1859 – also Zahlbruckner, 1941; Allan 1949); *S. urvillei* var. *flavicans* (Nylander 1860*b*, 1865, 1868*b*, 1888*b*; Lindsay, 1868; Krempelhuber, 1868, 1870, 1876*b*; Hue, 1890; Stizenberger, 1895); *S. endochrysa* var. *flavicans* (Müller Argoviensis, 1894; Cheel, 1914); and *Lobaria urvillei* var. *flavicans* (Hellbom, 1896) – while *Pseudocyphellaria flavicans* was used more recently (Martin, 1969*a*, 1969*b*; Galloway & James, 1980; Galloway, 1985*b*).

Pseudocyphellaria flavicans sens. str., differs from New Zealand material recorded under this name (see for example, Zahlbruckner, 1941; Allan, 1949; Murray, 1952; Martin, 1969*a*, 1969*b*; Martin & Child, 1972; Chin *et al.*, 1973; Galloway & James, 1977, 1980; Galloway *et al.*, 1983*b*; Galloway, 1985*b*) in both chemical and anatomical characters as earlier noted by Galloway & James (1977: 100). The Australasian vicariant of *P. flavicans* is thus *P. pickeringii*, which is discussed in detail below.

Morphology: Thallus orbicular or rosette-forming to irregularly spreading, 5–10(–20) cm diam., corticolous, terricolous or saxicolous, loosely to tightly attached centrally, margins ± free. *Lobes* very variable, usually ± rounded to rather ragged-incised, or complexly divided and imbricate, 0·5–1·5 cm wide, 0·5–2 cm long. *Margins* rarely entire, usually notched or incised, sinuous, becoming richly phyllidiate, sinuses inapparent, ± semicircular to imbricate. *Upper* *surface* bright emerald-green to glaucous-green when moist, pale yellow-green, to greyish yellow to tawny-ochre when dry, ± convex-undulate, shallowly wrinkled or pitted, occasionally irregularly faveolate, thin and brittle to ± coriaceous, matt or glossy, smooth or minutely scabrid-areolate in parts (×10 lens), soredia, maculae, and pseudocyphellae absent. *Isidia* mainly marginal, then occasionally spreading to lamina, minute, terete at first (0·1 mm tall or less), simple, soon bifurcating, becoming flattened-coralloid, phyllidiate or palmate-squamiform or ± pectinate, ± constricted at base, often forming a dense marginal crust spreading on to lamina and occasionally obscuring thallus. *Phyllidia* flattened, dorsiventral, upper surface convex, lower surface pale yellow, margins ridged, apices inflated, occasionally with minute, punctiform pseudocyphellae at margins and on lower surface, 0·1–3 mm tall. *Medulla* yellow. *Photobiont* green. *Lower surface* pale yellowish or yellow-white at margins, darker to ochre-brown or red-brown centrally, tomentose from margins to centre or with a narrow, glabrous, marginal zone, tomentum even, rather short, velvety, whitish, buff to red-brown. *Pseudocyphellae* yellow, flat to ± papillate-verruciform, scattered, fleck-like, round to irregular, 0·05–0·5 mm diam., sunk in tomentum, often inapparent, decorticate flat to convex. *Pycnidia* scattered, laminal, minute, punctate-impressed or ± papillate, 0·1 mm diam. or less, ostiole red-brown to black. *Apothecia* sparse to absent, sessile to ± subpedicellate, 0·2–5 mm diam., concave at first, then plane to convex-undulate at maturity, margins whitish, scabrid, ± involute at first, excluded at maturity, disc pale to dark red-brown, minutely papillate-roughened, epruinose, matt, exciple pale whitish-buff, translucent when moist, roughened to coarsely verrucose-areolate, occasionally short white-tomentose.

Anatomy: *Thallus* 160–230(–275) μm thick. *Upper cortex* 45–57 μm thick, upper 18–22 μm dilute yellow-brown or orange-brown, remainder colourless, cells compressed near surface, largest near photobiont layer, 4·5–15 μm diam. *Photobiont layer* 27–45 μm thick, photobiont green. *Medulla* 55–90 μm thick, colourless, hyphae 4·5 μm diam., encrusted with yellow crystals. *Lower cortex* 45–60 μm thick, cells colourless, 4·5–13·5 μm diam., tomental hairs to 5 μm thick, colourless, 20–130 μm long, rarely to 230 μm long, and occasionally with short, lateral branchlets. *Apothecia: Exciple* colourless to pale yellow-brown at margins, 130–185 μm thick, cells 4·5–13·5 μm diam., thick-walled. *Hypothecium* 35–45 μm thick, red-brown or pale brick-red, turning blue-green in K, deeper layers staining most strongly, zone near thecium olive-yellow. *Thecium* 70–80 μm tall, colourless; *epithecium* 7–11 μm thick, red-brown, strongly conglutinate, unchanged in K. *Asci* 72–80 × 15–18 μm. *Ascospores* colourless, 1-3-septate (rarely to 5-septate), fusiform-ellipsoid, apices pointed, cell contents sometimes markedly vacuolate, 2·5–29·5(–32) × 6·5–7 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, 2α, 3β, 22α-triacetoxystictane, 2α, 3β-diacetoxystictane-22-ol, stictane-3β-22α-diol, 2α-acetoxystictane-3β, 22α-diol, 3β-acetoxystictane-2α, 22α-diol, stictane-2α, 3β, 22α-triol, 3β, 22α-diacetoxystictane, 2α, 3β-diacetoxystictane-22-ol, 3β-acetoxystictane-22-ol.

Distinguishing features: *Pseudocyphellaria pickeringii* is a palaeotropical species widespread in New Zealand, forming irregular rosettes or spreading over bark, rock, and soil. It has variable, ± rounded to complexly divided, rather ragged, incised lobes, whose margins are ± isidiate-phyllidiate. The upper surface is coriaceous, smooth to faveolate in parts to ± scabrid-areolate (×10 lens), with marginal and laminal isidia (terete) and phyllidia (flattened-dorsiventral) present (Fig. 111). It has a yellow medulla, a green photobiont, and the lower surface is pale yellow to red-brown with a velvety tomentum, and scattered, yellow, often inapparent, pseudocyphellae. Apothecia are sparse or absent, though occasionally frequent in some specimens, sessile to subpedicellate with a conspicuous, whitish buff, coarsely verrucose-scabrid exciple. The hypothecium is red-brown, turning blue-green in K in fresh material. Spores are colourless, 1-3(-5)-septate, fusiform-ellipsoid. It has a complex chemistry of pigments and stictane triterpenoids (Chin *et al.*, 1973).

Variation: *Pseudocyphellaria pickeringii* occupies a wide variety of habitats in New Zealand. The ability to colonize different substrates in all areas of the country has led to a variety of

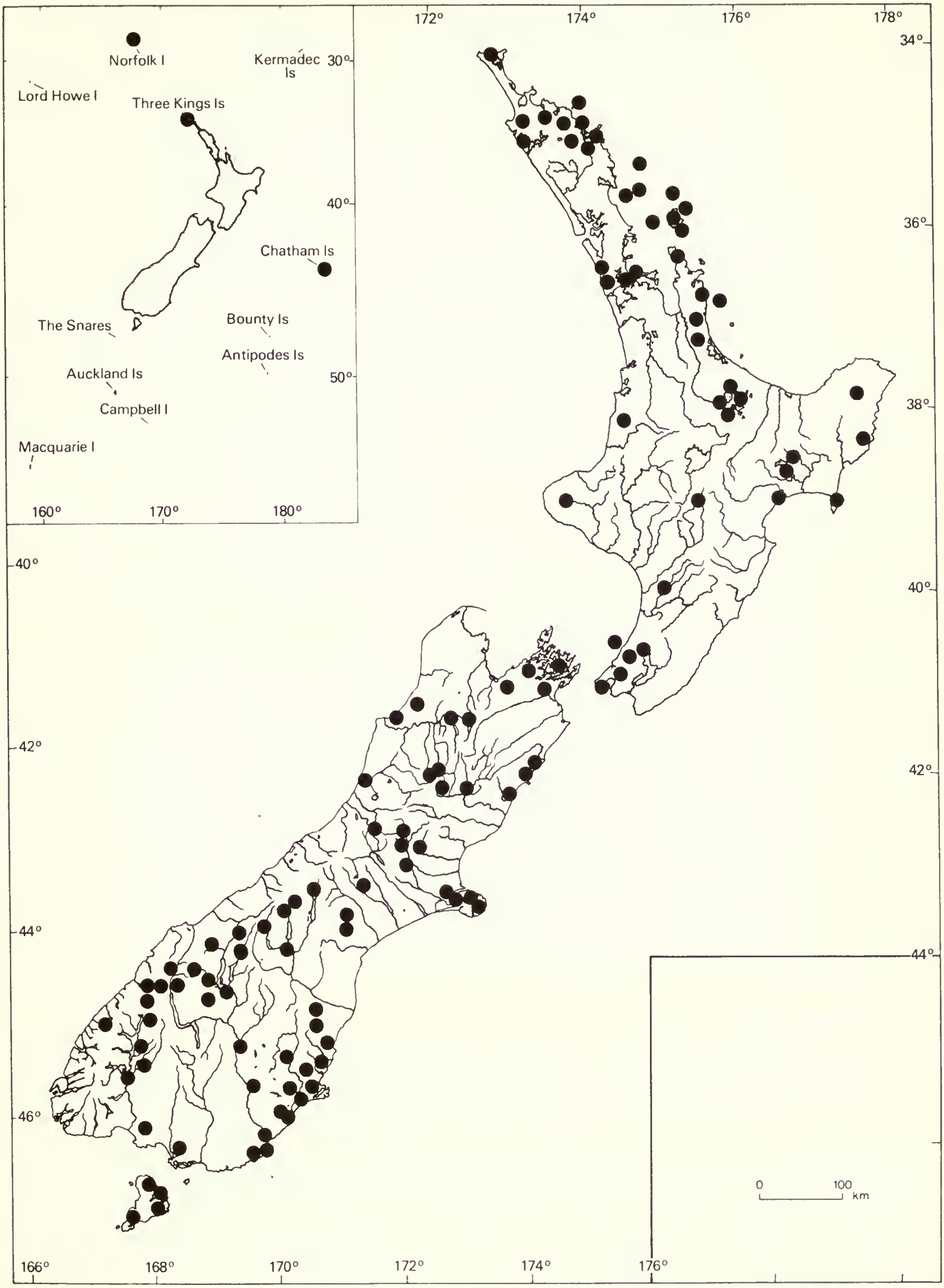

Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
Chatham Is
The Snares
Bounty Is
Antipodes Is
Auckland Is
Campbell I
Macquarie I
30°
40°
50°
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 112 Distribution of *Pseudocyphellaria pickeringii*.

morphologies though all are united by the yellow medulla and the laminal and marginal isidia which may become flattened-phyllidiate. There is some variation in thallus thickness, related to altitude and exposure to high light intensities, with subalpine forms being thicker and more coriaceous than shaded forest forms. Apothecia are very variable in number and are very often absent. The combination of a yellow medulla, green photobiont, and terete to flattened isidia at present unites a variety of forms found in Australasia, and in tropical regions, from the Malesian archipelago to Hawaii. Isidiate, yellow-medulla specimens of *Pseudocyphellaria* from New Guinea differ chemically from *P. pickeringii* and need closer evaluation. Tropical material is somewhat thinner, and more rosette-forming than specimens typically encountered in New Zealand. *P. pickeringii* varies from *P. flavicans* sens. str., in both anatomical and chemical characters. South American material of *P. flavicans* has consistently longer and thinner spores [(32–)34–43(–45) × 4·5–6 μm], and an orange-brown hypothecium that is unchanged in K, never turning blue-green as in new Zealand *P. pickeringii*. Further, its chemistry is different from *P. pickeringii*, containing fewer and different stictanes, confirming the suggestion made earlier, that New Zealand and South American populations of yellow-medulla isidiate species of *Pseudocyphellaria* are taxonomically separable (Galloway & James, 1977).

Pseudocyphellaria pickeringii is distinguished from the New Zealand endemic *P. degelii*, and from the southern South American *P. berberina*, both of which have entire margins and lack isidia, although *P. berberina* occasionally produces spasmodic marginal lobules. There are also chemical differences between *P. pickeringii* and *P. degelii* (Goh *et al.* 1978); between *P. pickeringii* and *P. berberina*; and between *P. degelii* and *P. berberina* (Wilkins, 1977*b*). *Pseudocyphellaria nermula*, a restricted New Zealand endemic is similar to *P. pickeringii* but has a blue-green photobiont and marginal phyllidia, and it never produces terete isidia. The northern coastal palaeotropical species *P. poculifera* is distinct from *P. pickeringii* in having fragile, marginal, sorediate isidia and distinctive, pedicellate apothecia with ragged-erose-sorediate margins and an exciple concolorous with the thallus.

Distribution: (Fig. 112) Widespread from the Three Kings Is (lat. 35°6′S) to Stewart I., and the Chathams, coastal to subalpine, sea-level to 1200 m.

Habitat ecology: Pseudocyphellaria pickeringii, a readily dispersed lichen, occupies a wide range of habitat niches in New Zealand, from coastal scrub to subalpine tussock (*Chionochloa*) grassland. It also grows on a variety of rock substrates (lava, basalt, greywacke, schist), and on soil on the forest floor or beneath successional shrubs (especially *Leptospermum*). It will colonize both bark and twigs of a number of forest trees and shrubs, and it is especially common on beech (*Nothofagus*) bark. *Pseudocyphellaria pickeringii* flourishes in medium to high-light habitats but will also tolerate moderate shade. It is known from the following phorophytes: *Aristotelia serrata*, *Beilschmiedia tawa*, *Cordyline australis*, *Griselinia littoralis*, *Kunzea ericoides*, *Leptospermum scoparium*, *Melicytus ramiflorus*, *Myrsine divaricata*, *Metrosideros excelsa*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Olearia fragrantissima*, *Podocarpus hallii*, *P. totara*, *Rhopalostylis sapia*, and *Vitex lucens*.

Specimens examined: 240.

43. **Pseudocyphellaria poculifera** (Müll. Arg.) D. Galloway & P. James **Fig. 113**

in *Lichenologist* **12**: 301 (1980). – *Sticta poculifera* Müll. Arg. in *Flora, Jena* **65**: 304 (1882). Type: Lord Howe Island, Mt Gower, *F. v. Mueller* (G 002123! – holotype; BM!, MEL! – isotypes).

Morphology: Thallus rosette-forming to irregularly spreading, 3–8(–12) cm diam., loosely attached centrally, ± subascendent and free at margins, corticolous, rarely saxicolous. *Lobes* somewhat dissected-laciniate, 4–10 cm wide and 10–40 mm long, discrete and incised-pectinate at margins, contiguous lobes ± consistently discrete, rarely imbricate, branching very irregular, shallowly to deeply lacerate. *Margins* slightly thickened below, sinuous, subascendent, uneven, crenate, to irregularly notched, often torn or ragged, ± eroding to lower surface, furnished with fine, delicate, ± coralloid pseudoisidia, often distinctly white-tomentose in absence of isidia, tomentum thin, silky. *Upper surface* bright lettuce-green or emerald-green to dark-green when

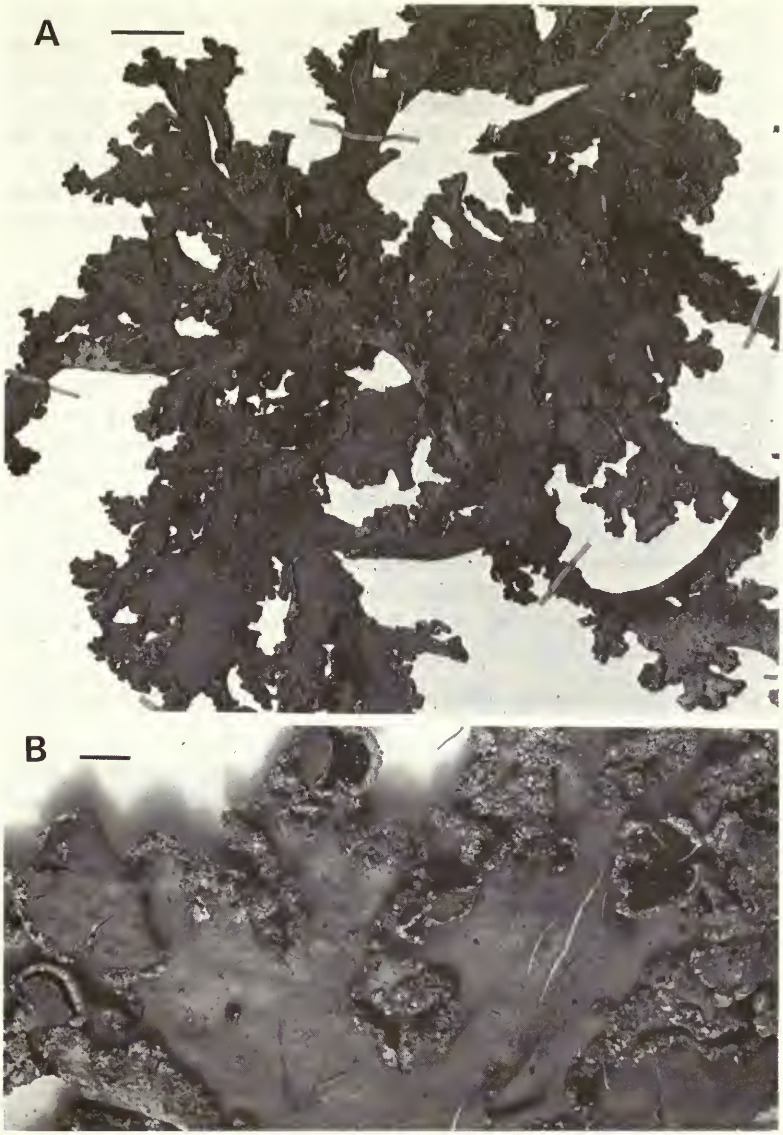


Fig. 113 *Pseudocyphellaria poculifera*. Hen Island, *B. W. & G. C. Hayward* (AK 164446) A. Scale = 1 cm. B. Scale =1 mm.

wet, pale glaucous-buff when dry becoming brick-red or red-brown on storage in the herbarium, undulate, obscurely wrinkled or pitted in parts, not faveolate, internal cephalodia visible as hemispherical swellings; matt, often somewhat coriaceous, minutely scabrid-areolate in parts (× 10 lens) especially towards apices, also sometimes conspicuously minutely pubescent at margins and on large areas of upper surface, tomentum fine, silky, white, best seen at lobe margins (× 10 lens). *Isidia* greenish yellow, mainly marginal (rarely on upper surface regenerating from cracks or holes), densely clustered, minutely coralloid, ± corticate but soon eroding and appearing sorediate. Maculae and pseudocyphellae absent. *Medulla* yellow. *Photobiont* green, ?*Dictyochloropsis*. *Lower surface* pale buff, brownish or pinkish centrally, yellowish at margins becoming distinctly reddish on storage in the herbarium, irregularly tomentose, tomentum white, silky, ± dense in parts at margins, elsewhere entirely glabrous from margins to centre, coarsely to finely wrinkled, often minutely faveolate at margins. *Pseudocyphellae* yellow, conspicuous, scattered, frequent, 0·1–0·5(–1) mm diam., round to irregular, to ±

effigurate-sigmoid, often ± erose, decorticate area flat or shallowly concave, sometimes developing granular pseudoisidia. *Apothecia* moderately common, marginal to submarginal, solitary, most commonly developed at lobe apices, distinctly pedicellate, pedicel 0·5–2 mm wide and tall, insertion of pedicel making a distinctive concavity on the lower surface, margins entire to irregularly sinuous, granular-isidiate, often eroding and exposing yellow medulla, (1–)2–6(–10) mm diam., exciple concolorous with thallus, conspicuously white-tomentose at first, becoming coarsely scabrid-areolate at maturity, disc matt, red-brown when wet, brown-black when dry, epruinose. *Pycnidia* common on lower surface, hemispherical, with a black, apical dimple, 0·2–0·5 mm diam.

Anatomy: *Thallus* 140–165(–200) μm thick. *Upper cortex* 35–75 μm thick, colourless to pale straw, outermost 4–7 μm of necrotic cells. *Photobiont layer* 18–25 μm thick, *photobiont* green, ?*Dictyochloropsis*. *Medulla* very compact, 40–70(–90) μm thick, hyphae 2·5–3·5 μm diam., encrusted with yellow-brown crystals. *Lower cortex* 14–22(–30) μm thick, colourless to pale straw, cells 5–9 μm diam. *Tomental hairs* colourless, 7 μm thick, central canal conspicuous, simple, solitary or in fascicles of 2–6, 20–90 μm long. *Apothecia: Exciple* containing photobiont and comprising cortex, photobiont layer, and medulla as in vegetative thallus. *Hypothecium* pale brown-pink, 20–35 μm thick, well delimited from medulla. *Thecium* colourless to pale straw, 45–60(–65) μm tall; *epithecium* 4·5–7 μm thick, dilute red-brown, paler in K. *Asci* 50–55 × 15–18 μm. *Ascospores* pale to dark red-brown, biseriate, broadly fusiform-ellipsoid, straight or slightly curved, apices pointed, 3-septate at maturity, central locules normally largest, though sometimes rather uneven-irregular to ± compressed with end locules being larger, locule contents often oily-granular and vacuolate, (18–)20–23(–25) × 5·5–7·5 μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, sterols, and unidentified ?fernene triterpenoids.

Variation: *Pseudocyphellaria poculifera* is a rather constant species and varies mainly in the morphology of the lobe margins and their associated delicate, ± coralloid isidia. Specimens from Lord Howe Island (type locality), from New Caledonia, and from Fiji have slightly more lacerate-indented lobe margins than do the New Zealand collections, but in all other respects populations are identical. Some New Zealand specimens have strongly eroded marginal isidia but the morphology of the resulting apparent soralia is different from the characteristic labriform-linear soralia seen in *P. aurata* (to which *P. poculifera* is most closely related), being lacerate-incised or ragged. The thallus of *P. poculifera* is thinner than that of *P. aurata*, and individuals are much more commonly fertile than their sorediate counterpart species. There are also anatomical differences between the two, with the hymenium and hypothecium of *P. aurata* being taller than the corresponding tissues in *P. poculifera*, and the spores of *P. poculifera* being shorter than those of *P. aurata*.

P. poculifera is distinguished from *P. rubella* by the lack of laminal soredia and surface tomentum, and from *P. pickeringii* in the nature of the isidia, the structure of the exciple, and in the size and colour of the spores; those of *P. poculifera* being red-brown while those of *P. pickeringii* are colourless. In addition, there are major chemical differences separating these species, *P. poculifera* producing sterols and unidentified fernene triterpenoids, *P. rubella* producing lupane triterpenoids, and *P. pickeringii*, stictane triterpenoids.

Distribution: (Fig. 114) From the Three Kings Is (lat. 34°S), southwards in mainly lowland, coastal habitats to Kopu, southern Coromandel Range (lat. 37°S); sea-level to 300 m. Known from the following offshore islands: Three Kings Is, Cavalli Is, Paeroa, and Poroporo Is (Bay of Islands), Poor Knights Is, Hen I., Great Barrier I., and Rakitu I. It is noteworthy that *P. poculifera* appears not to have increased its range south of the Auckland isthmus, an important geographical barrier which has at various times (most recently during high interglacial sea levels) been breached by a strait isolating the North Auckland Peninsula (Fleming, 1979*c*).

It is also known from Queensland in Australia, Lord Howe I., New Caledonia, and Fiji.

Habitat ecology: *Pseudocyphellaria poculifera* colonizes both twigs and bark of the following

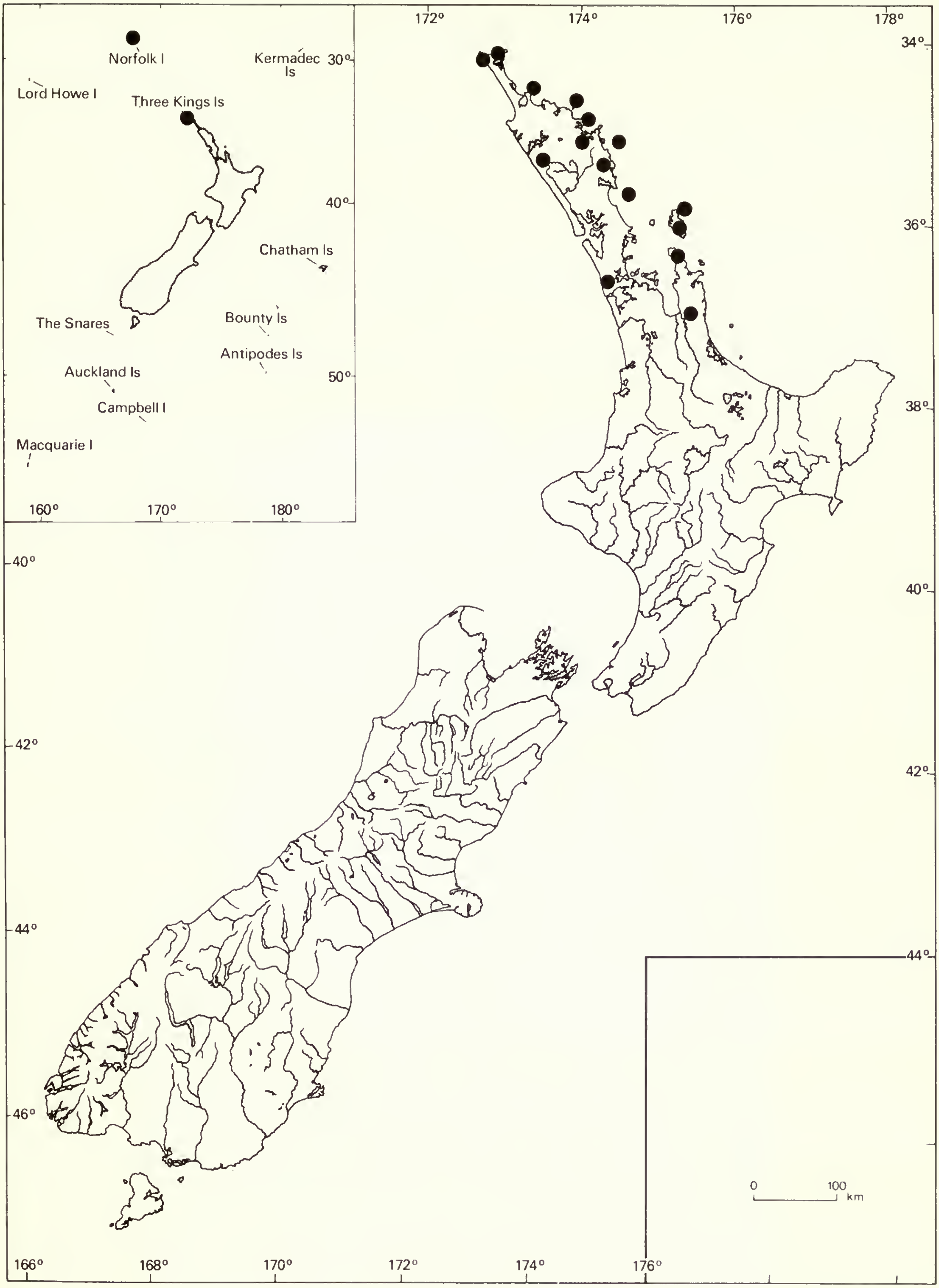

Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
30°
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
50°
Auckland Is
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
34°
36°
38°
40°
42°
44°
46°
40°
42°
44°
46°
0
100
km
166°
168°
170°
172°
174°
176°

Fig. 114 Distribution of *Pseudocyphellaria poculifera*.

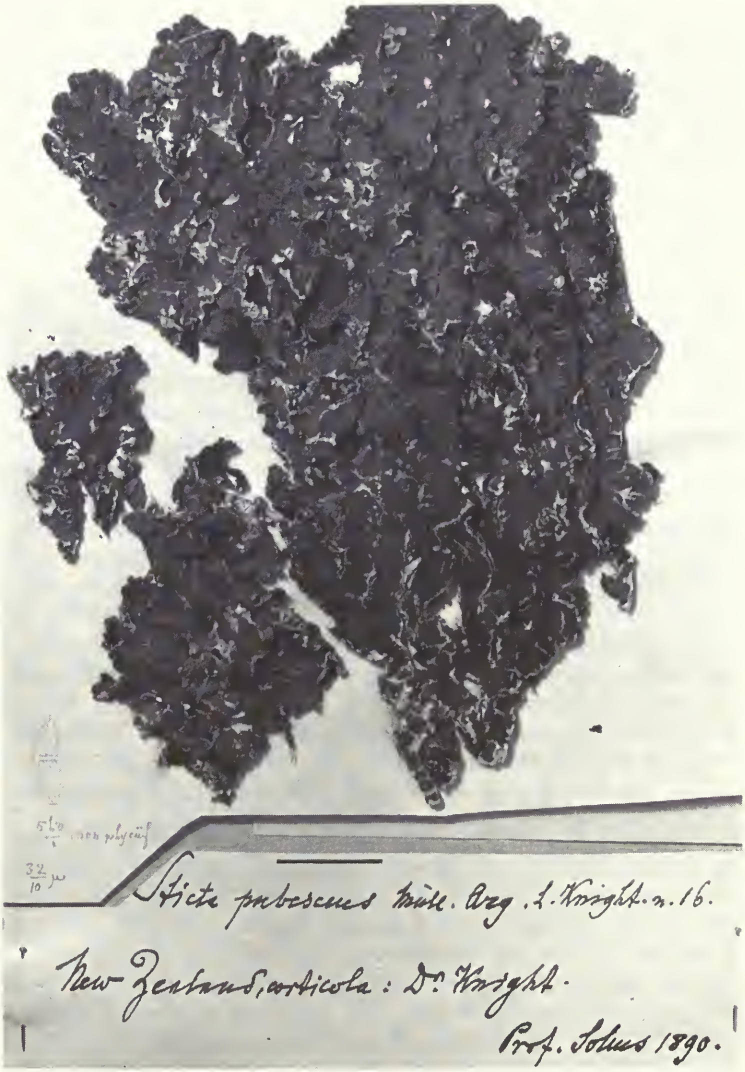
phorophytes: *Coprosma rhamnoides*, *Cordyline australis*, *C. kaspar*, *Kunzea ericoides*, *Leptospermum scoparium*, *Melicytus ramiflorus*, *Litsaea calicaris*, *Myrsine australis*, *Metrosideros excelsa*, and *Sphaeropteris medullaris*. Although primarily a bark and twig species, it is occasionally collected from rocks beneath *Kunzea ericoides* on some offshore islands. It is a photophilous species in northern, coastal forest favouring similar conditions to *P. aurata* and associating with the same group of lichens in such habitats as does *P. aurata*.

Specimens examined: 28.

44. Pseudocyphellaria pubescens (Müll. Arg.) D. Galloway & P. James **Fig. 115**

in *Lichenologist* **12**: 302 (1980). – *Sticta pubescens* Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31**: 28 (1892). – *Lobaria pubescens* (Müll. Arg.) Hellbom in *Bih. K. svenska Vetensk. – Akad. Handl.* **21**(3/13): 41 (1896). – *Sticta muelleriana* Zahlbr., *Cat. Lich. Univ.* **3**: 356 (1925). Type: New Zealand, sine loco, *C. Knight* (G! – holotype).

Sticta grandis Stirton in *Trans. N.Z. Inst.* **31**: 72 (1900). Type: New Zealand, Canterbury, Oxford Bush, *T. W. N. Beckett* (BM! – holotype, CHR! – isotype).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32/10 μ
Sticta pubescens Müll. Arg. l. Knight n. 16.
New Zealand, corticola: Dr. Knight.
Prof. Solms 1890.

Fig. 115 *Pseudocyphellaria pubescens*. Holotype of *Sticta pubescens* (G). Scale = 2 cm.

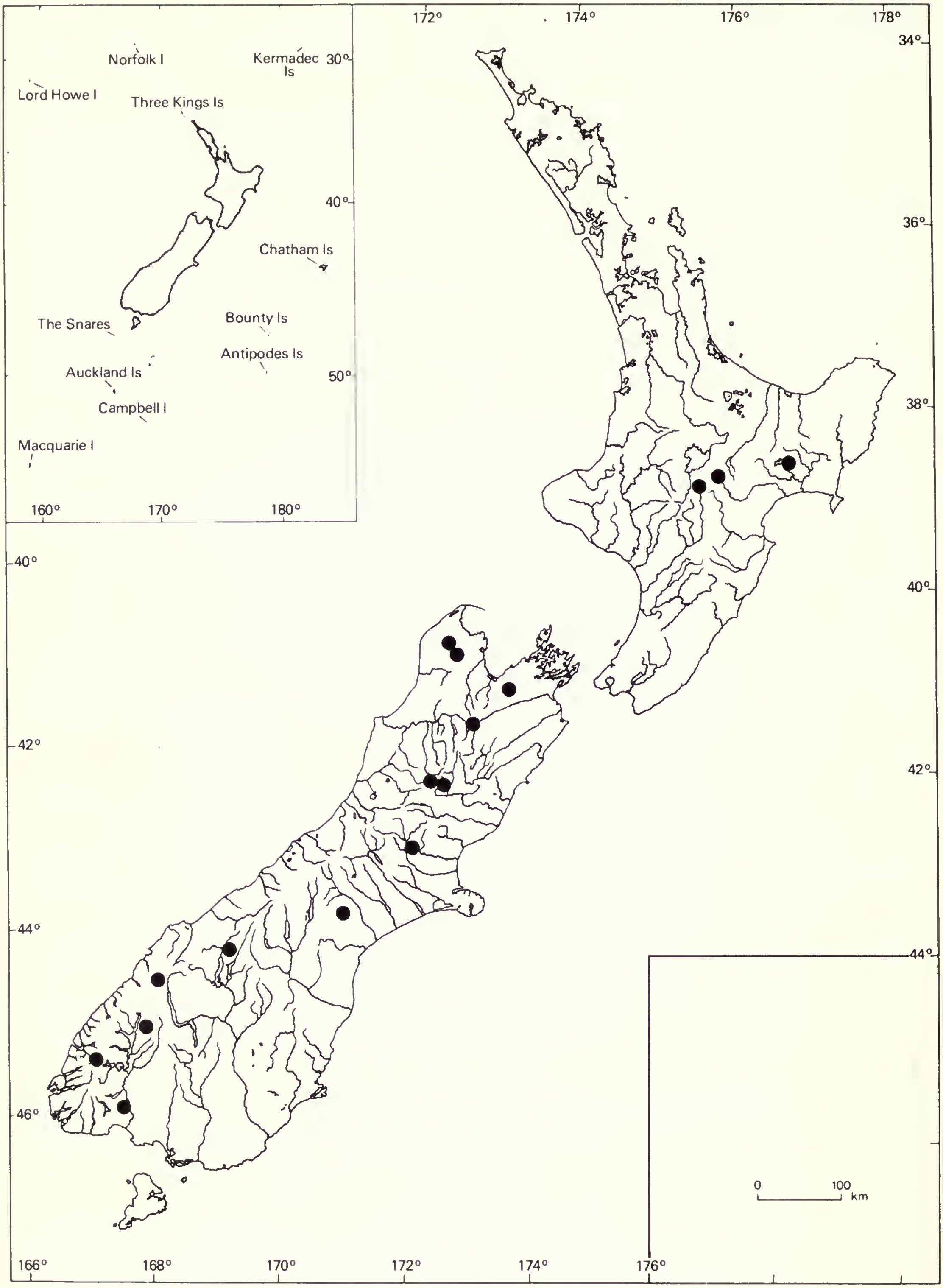
Zahlbruckner (1925: 356) in publishing a new name [*Sticta muelleriana*] for *S. pubescens* is in error, since Persoon (1827: 199) never published *Sticta pubescens* as Zahlbruckner states in the *Catalogus*. Rather, he described *Parmelia pubescens*, which is a synonym of the South American taxon *Pseudocyphellaria endochrysa* (Galloway, 1986*a*).

Morphology: Thallus orbicular to irregularly spreading, 5–15(–25) cm diam., loosely to closely attached centrally, margins ± free, corticolous. *Lobes* convex to shallowly concave, linear-elongate to rounded, 0·5–1(–1·5) cm wide, 1–4 cm long, subdichotomously branching, apices ± imbricate, rarely discrete, central parts complex-imbricate. *Margins* entire, shallowly notched, incised or ± crenate in parts, sinuous, slightly ascending, distinctly thickened, glabrous to tomentose, rounded to ± revolute in parts, occasionally with slightly projecting, yellow, scattered, pseudocyphellae or with thalline lobules, sinuses semicircular. *Upper surface* bright apple-green to glaucous-green when moist, olivaceous to yellow-brown or tawny when dry, coarsely areolate-scabrid (× 10 lens), cracked or smooth to ± entirely tomentose or glabrous, tomentum restricted to margins and rather patchy elsewhere, weakly wrinkled or pitted to shallowly and irregularly faveolate, coriaceous, tough, smooth and glossy in parts to roughened-areolate, tomentum very variable, white, glistening, long (0·2–1 mm), thinly scattered to thickly and densely developed, soredia, isidia, maculae, phyllidia, and pseudocyphellae absent. *Medulla* white. *Photobiont* green. *Lower surface* densely tomentose from margins to centre, pale yellowish buff at margins, becoming darker centrally, tomentum woolly-arachnoid, whitish, silky. *Pseudocyphellae* yellow, conspicuous, common, scattered, round to irregular, 0·05–0·2 mm diam., shallowly verruciform, decorticate area flat or subconvex, sunk in tomentum. *Pycnidia* occasional to common, laminal, scattered, shallowly papillate, 0·1–0·2 mm diam., central ostiole red-brown to black, punctate-depressed. *Apothecia* marginal or submarginal, rare to occasional, pedicellate from soon after emergence, pedicel stout, 0·5–1 mm tall and to 1 mm wide, concolorous with thallus, coarsely verrucose-scabrid, solitary, or clustered in groups, 3-5-together, (0·5–)1–5(–8) mm diam., cupuliform and deeply concave at first, disc obscured by excipular tissue, shallowly concave, plane or ± undulate at maturity, disc dark red-brown to black with a fine, greyish pruina when young and often persisting in mature fruits, smooth, matt or minutely granular, exciple containing photobiont, concolorous with thallus to whitish buff, translucent when moist, coarsely reticulate-scabrid-areolate, pyramidal wedges of cells forming crenate-dentate margins to disc.

Anatomy: Thallus 310–500 µm thick. *Upper cortex* 45–68 µm thick, surface very irregular-roughened-scabrid, upper 22–27 µm pale straw-yellow, remainder colourless, cells 2·5–7 µm diam. *Tomental hairs* to 5 µm diam., 45–155 µm long. *Photobiont layer* 45–55 µm thick, *photobiont* green, *Dictyochloropsis*, cells to 7 µm diam. *Medulla* 135–260 µm thick, colourless. *Lower cortex* pale straw-yellow, 27–32 µm thick, cells 4·5–17 µm diam. *Tomental hairs* straw-yellow to brown, to 7 µm diam., 45–140(–260) µm long, in fascicles. *Apothecia: Exciple* colourless to pale yellow-brown at margins, 110–185 µm thick, cells 4·5–11·5 µm diam. *Hypothecium* 82–90 µm thick, pale yellow-brown, slightly intensifying in K. *Thecium* 100–110 µm thick, colourless; *epithecium* 7–11·5 µm thick, olive-brown to yellow-brown, granular, colour dissolving in K. *Asci* 77–90 × 13·5–18 µm. *Ascospores* smoky grey-brown, thickened 1-septate, septum to 2·5 µm thick, to 3-septate, straight or curved, fusiform-ellipsoid, apices pointed, 23–27 × 7–9 µm.

Chemistry: methyl evernate (tr.), tenuiorin, methyl lecanorate (tr.), methyl gyrophorate, gyrophoric acid (tr.), hopane-15α, 22-diol, hopane-6α, 7β, 22-triol, an unidentified triterpenoid, norstictic (tr.), salazinic (tr.), stictic, cryptostictic, and constictic acids, an unidentified depsidone, and traces of pulvinic acid, pulvinic dilactone, and calycin.

Distinguishing features: Pseudocyphellaria pubescens is an endemic species having linear-elongate to ± rounded, thick, coriaceous lobes, with entire to crenate margins which are often ± tomentose. The upper surface is coarsely areolate-scabrid, wrinkled-pitted to irregularly faveolate, ± glabrous to entirely tomentose. It has a white medulla, a green photobiont, and a pale buff, densely tomentose lower surface, with conspicuous, yellow pseudocyphellae.


Norfolk I
Kermadec Is
Lord Howe I
Three Kings Is
30°
40°
Chatham Is
Bounty Is
The Snares
Antipodes Is
Auckland Is
50°
Campbell I
Macquarie I
160°
170°
180°
172°
174°
176°
178°
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36°
38°
40°
42°
44°
46°
40°
42°
44°
46°
166°
168°
170°
172°
174°
176°
0
100
km

Fig. 116 Distribution of *Pseudocyphellaria pubescens*.

Apothecia rare to occasional, marginal, pedicellate, disc dark red-brown to black, white-pruinose when young. Spores grey-brown, thickened 1-septate to 3-septate. The chemistry is characteristic, containing an unusual combination of hopane triterpenoids, pigments, depsidones, and metabolites of the stictic acid complex.

Variation: *Pseudocyphellaria pubescens* has a rather variable morphology, the lobes varying in width and length from elongate-laciniate with subdichotomous branching and ± discrete from margins to centre, to short and rounded, complexly divided, imbricate. The tomentum of the upper surface and margins is also rather variable in density and position, with some forms being entirely and densely tomentose, while others have only scattered patches of tomentum with most of the lobes and margins being ± glabrous. The pruinosity of the apothecial discs is also rather variable, being consistently present in young, recently expanded discs, but only very spasmodically present on mature apothecia.

Pseudocyphellaria pubescens is distinguished from *P. coriacea* by the irregularly wrinkled to ± faveolate upper surface, the yellow pseudocyphellae, and the complex chemistry. It is distinct chemically and morphologically from the delicately isidiate, tomentose species *P. gretae* which has white pseudo-cyphellae and a negative chemistry. In several earlier accounts (Martin, 1966, 1969*a*; Martin & Child, 1972; Galloway & Simpson, 1978) *P. pubescens* was recorded as *P. obvoluta*, a southern South American, hirsute species which has marginal, broadly rounded, flabellate lobes, marginal apothecia with red-brown, epruinose discs, and a different chemistry (Galloway, 1986*a*). *Pseudocyphellaria pubescens* occasionally forms photosymbiodemes with *P. margaretiae* (Renner & Galloway, 1982).

Distribution: (Fig. 116) North I., from lat. 39°S southwards in Urewera National Park, Kaweka and Kaimanawa Ranges, and in South I., from Nelson to Fiordland mainly close to and east of Main Divide, montane to subalpine, 200–1050 m.

Habitat ecology: *Pseudocyphellaria pubescens* is primarily a forest species in cool, humid habitats with moderate light and high rainfall. Mainly an epiphyte of beech (*Nothofagus fusca*, *N. menziesii*, and *N. solandri* var. *cliffortioides*), it often forms very large rosettes (to 25 cm diam.) in open beech forest, close to or at forest margins though it is also known from subalpine serpentine (Cobb Valley, Nelson); it is an epiphyte of the trunks of the following phorophytes: *Dacrycarpus dacrydioides*, *Griselinia littoralis*, *Pseudopanax simplex*, *Podocarpus totara*, and *Prumnopitys taxifolia*.

Specimens examined: 26.

45. **Pseudocyphellaria rubella** (J. D. Hook. & Taylor) D. Galloway & P. James **Fig. 117**

in *Lichenologist* **12**: 302 (1980). – *Sticta rubella* J. D. Hook. & Taylor in *Hook. Lond. J. Bot.* **3**: 649 (1844). – *Crocodia rubella* (J. D. Hook. & Taylor) Trevisan, *Lichenotheca veneta* exs. 75 (1869). – *Lobaria rubella* (J. D. Hook. & Taylor) Kuntze, *Revis. gen. pl.* **2**: 876 (1891). Type: Van Diemen's Land (Tasmania), St Patrick's River, on granite, *Gunn* (BM! – lectotype).

Parmosticta purpurascens Stirton in *T.N.Z.I.* **32**: 71 (1900). – *Sticta purpurascens* (Stirton) Zahlbr., *Cat. Lich. Univ.* **3**: 362 (1925). Type: Australia, Blue Fier, Herb. *Baron v. Mueller*, ex Herb. Stirton (BM! – lectotype) [see Rogers (1983)].

Morphology: *Thallus* orbicular, ± rosette-forming to irregularly spreading and straggling, 5–10(–15) cm diam., closely attached centrally, margins ± loose and free to ascending, corticolous, rarely saxicolous. *Lobes* variable, linear-elongate to somewhat irregular rounded, discrete at margins, imbricate to plicate-complex centrally. *Margins* crenate-ragged, incised, notched, torn or ± lobulate, sometimes sinuous and ± ascending, conspicuously white-tomentose, often eroded-yellow-sorediate or with punctiform to ± linear, yellow pseudocyphellae, occasionally ± involute, slightly thickened below, sinuses irregular. *Upper surface* bright lettuce-green when moist, pale pinkish buff to reddish on storage, otherwise pale green-grey, undulate, shallowly faveolate or ± wrinkled in parts, occasionally ± fenestrate or reticulate-cracked, tomentose from margins to centre, occasionally ± glabrous centrally and

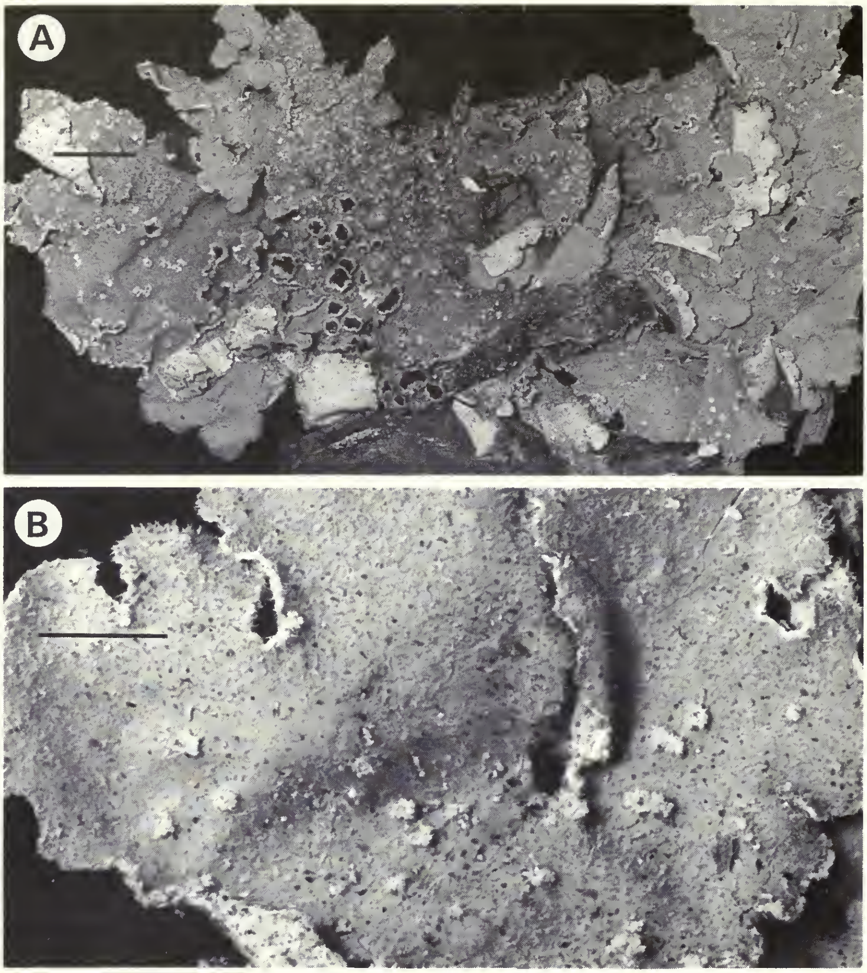


Fig. 117 *Pseudocyphellaria rubella*. West Bay, Lake Rotoiti, Nelson, *Galloway* (CHR 358611). A. Scale = 1 cm. B. Scale = 5 mm.

tomentose at margins, tomentum white, silky, rather fine, short, thin or thick, sorediate, without isidia, maculae, phyllidia or pseudocyphellae. *Soredia* in marginal, linear to sublinear or discrete, labriform soralia, in laminal, punctiform to ± confluent, ± rounded to irregular, erose or pustular soralia, soredia coarse, granular, yellow, often covering large areas of thallus. *Medulla* yellow. *Photobiont* green. *Lower surface* pale yellow-white to pale buff, rarely brownish centrally, ± glabrous or minutely pubescent to densely tomentose, tomentum white, silky. *Pseudocyphellae* prominent, yellow, numerous, flat or very shallowly convex, papillate 0·05–0·3 mm diam., often sunk in tomentum. *Pycnidia* infrequent, laminal, scattered, minute, 0·1 mm diam. or less, papillate, red-brown to black. *Apothecia* rather rare, submarginal to laminal, pedicellate, round to somewhat irregular, 1–6 mm diam., distinctly cupuliform at first then plane or shallowly concave, disc dark red-brown to brownish black, matt or roughened-granular, epruinose, plane to somewhat undulate, margins irregular, crenate-lobulate and somewhat involute, usually ± eroded, granular, yellow-sorediate, exciple concolorous with thallus, coarsely corrugate-scabrid, tomentose, with scattered, verruciform, to pustular yellow soralia.

Anatomy: *Thallus* 125–300 μm thick. *Upper cortex* 18–27 μm thick, pale straw-yellow to colourless, upper surface very uneven, cells thick-walled, 4·5–6·5 μm diam. *Tomental hairs* to 7 μm diam., 40–100(–180) μm long. *Photobiont layer* 25–45 μm thick, *photobiont* green, cells tightly packed, to 7 μm diam. *Medulla* 65–115(–200) μm thick, hyphae to 4·5 μm diam., densely encrusted with yellow crystals. *Lower cortex* 18–25 μm thick, colourless to pale straw-yellow, cells 4·5–7 μm diam. *Tomental hairs* colourless, 40–130(–190) μm long and 4·5–7 μm diam., in fascicles of 3–12. *Apothecia: Exciple* containing photobiont cells, cellular, colourless, cells 6–11·5 μm diam., in discrete pyramidal groups 10–45 μm thick and 25–45 μm wide at margins. *Hypothecium* 25–45 μm thick, opaque, red-brown. *Thecium* 100–135 μm tall, colourless; *epithecium* 6·5–14 μm thick, dark olive-grey to brown. *Asci* 65–74 × 16–18 μm. *Ascospores* brown, 3-septate, ellipsoid, septa thick, locules oblong to ± triangular in section, 25–34(–38·5) × 9–11(–14) μm.

Chemistry: Pulvinic acid, pulvinic dilactone, calycin, and 20 lupane derivatives viz., 3β-acetoxylupan-29-al, 3β-acetoxylupan-20-ol, (29RS)-3β-hydroxylupan-29-al, (20RS)-3β-hydroxylupan-20-oic acid, (20RS)-3β-acetoxylupan-20-oic acid, lupan-3β, 20-diol, (20RS)-lupan-3β, 29-diol, (20RS)-30-norlupane-3β, 20;diol, (20RS)-lupane-3β, 20, 29-triol, (20RS)-3β-acetoxylupane-20, 20-diol, 3β-acetoxylup-20(29)-ene, 3β-acetoxy-30-norlupan-20 -one, 3β-acetoxylup-20(29)-en-30-ol, 3β-hydroxy-30-norlupan-20-one, 3β-hydroxylup-20(29) -ene (lupeol), lup-20(29)-en-3β, 30-diol, 20, 29, 30-trinorlupane-3β, 19α-diol, 3β, 19α-diacetoxy-20, 29, 30-trinorlupane, 3β-acetoxylupan-20(29)-epoxide, and 3β-hydroxylupan-20(29)-epoxide.

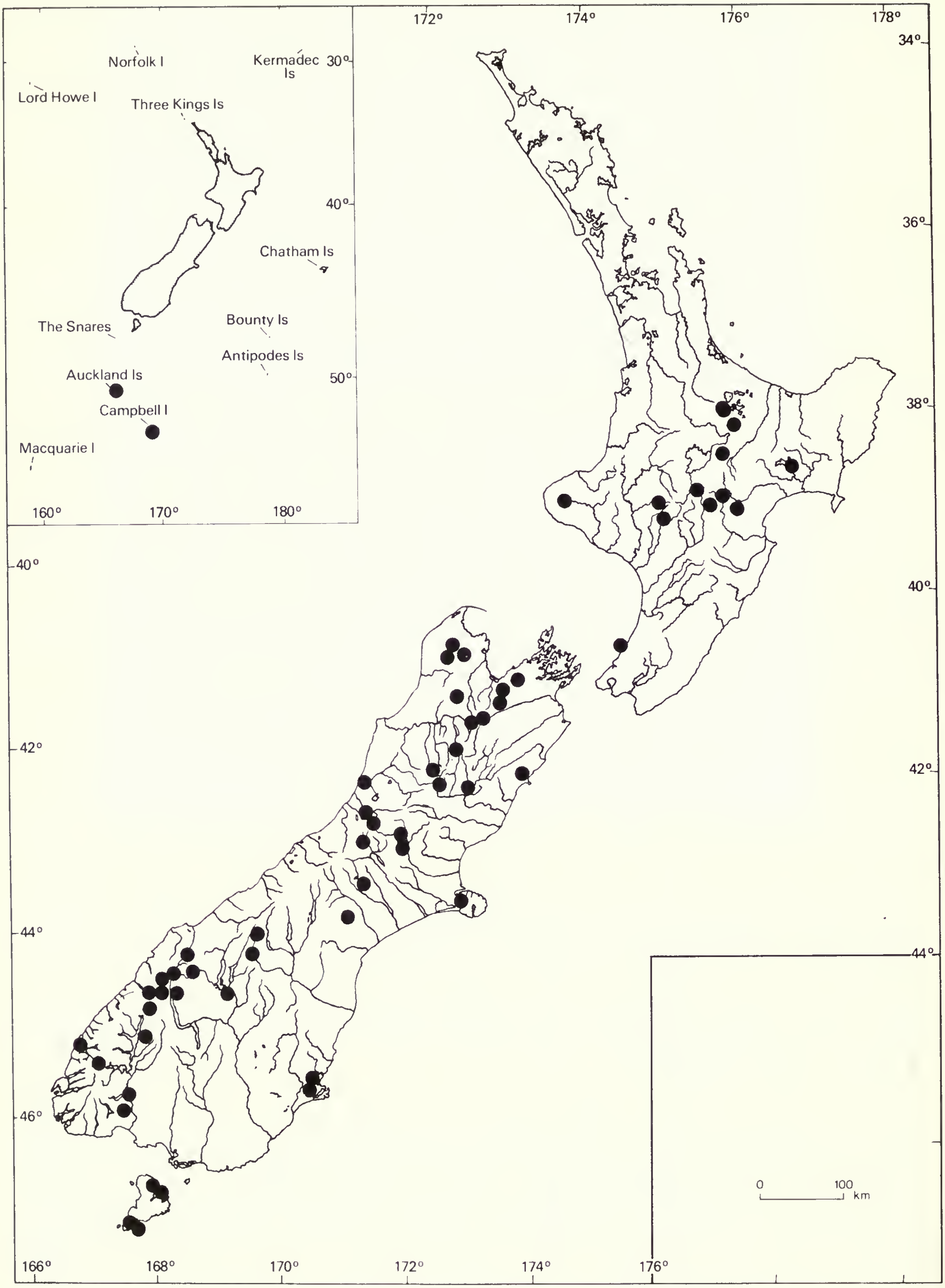
Distinguishing features: Pseudocyphellaria rubella is an Australasian species having ± linear-elongate to somewhat rounded lobes, with irregularly incised, rather ragged, tomentose margins. The upper surface is undulate to irregularly reticulate-faveolate, ± tomentose, sorediate (Fig. 114B). Soralia are marginal (linear or discrete or labriform) and/or laminal (punctiform to confluent, round to irregular), the soredia coarse, granular, yellow. It has a yellow medulla, a green photobiont, and a pale yellow-buff lower surface, with numerous, prominent, yellow pseudocyphellae. Apothecia rather rare, pedicellate, exciple concolorous with thallus, corrugate-scabrid, tomentose. Spores brown, 3-septate. It has a complex chemistry containing pigments and *c.* 20 lupane triterpenoids.

Variation: Pseudocyphellaria rubella is a characteristic, ± rosette-forming species which shows little morphological variation throughout its range. The upper surface ranges from smooth to faveolate and the tomentum from thick, silky, and uniform to rather scattered and patchy, though the lobe margins are nearly always tomentose. The species is distinguished by the laminal tomentum and the laminal, rounded-erose soralia, characters which separate it from *P. aurata* which has linear, labriform soralia and a glabrous upper surface; and also from *P. poculifera* which has ragged-isidiate margins. It is distinguished from the South American tomentose species *P. pilosella* which has a different chemistry (Galloway, 1986*a*), a blue-green photobiont, and no soredia, and from the sorediate *P. piloselloides* which has a blue-green photobiont, a different chemistry (Galloway, 1986*a*), and submonophyllous to indented-lacerate or ragged lobes which are shallowly faveolate near the margins.

Distribution: (Fig. 118) North I., south of Rotorua (lat. 38°S) to Wellington (Kapiti I.), and in South I., from Nelson to Fiordland, and eastwards from Marlborough to Otago (Dunedin). Also on Stewart I., from Mt Anglem to Port Pegasus, and on the Auckland Is, and Campbell I., lowland to subalpine, sea-level to 1500 m.

Habitat ecology: Pseudocyphellaria rubella is a photophilous species found commonly on beech (*Nothofagus*) bark, and on successional shrubs (especially *Leptospermum*) at forest margins, and in scrub associations from near sea coasts to above treeline. It is most common in beech forests in moderate to high-rainfall areas, but will also colonize old stumps, serpentine rock, and rarely, introduced trees (*Populus* in a plantation at Hanmer State Forest). It is known from the following phorophytes: *Aristotelia fruticosa*, *Coprosma rhamnoides*, *Cyathea*, *Dracophyllum filifolium*, *D. longifolium*, *Elaeocarpus hookerianus*, *Kunzea ericoides*, *Leptospermum scoparium*, *Nothofagus fusca*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Plagianthus regius*, *Podocarpus hallii*, *P. totara*, *Prumnopitys taxifolia*, and *Senecio eleagnifolius*.

Specimens examined: 80.


Norfolk I
Kermadec Is
30°
Lord Howe I
Three Kings Is
40°
Chatham Is
The Snares
Bounty Is
Antipodes Is
50°
Auckland Is
Campbell I
Macquarie I
160°
170°
180°
172°
174°
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34°
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42°
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170°
172°
174°
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Fig. 118 Distribution of *Pseudocyphellaria rubella*.

46. Pseudocyphellaria rufovirescens (Church. Bab.) D. Galloway **Fig. 119**

in *Mycotaxon* **16**: 205 (1982). – *Sticta richardi* var. *rufovirescens* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 278 (1855). Type: New Zealand, Akaroa, ? *Hombron* (BM ex PC! – lectotype) [see note 1].

Sticta richardi var. *glauca* Church. Bab. in J. D. Hook., *Fl. nov.-zel.* **2**: 278 (1855). – *Pseudocyphellaria richardi* var. *glauca* (Church. Bab.) Räsänen in *Annls Bot. Soc. zool.-bot. fenn. Vanamo* **2** (1): 39 (1932). Type: *S. impressa* Taylor pr. p. – no specimen cited.

Sticta fossulata f. *pallida* Krempelh. in *Verh. zool.-bot. Ges. Wien* **26**: 446 (1876). Type: New Zealand, Auckland, *Dr Wawra* 315 (M! – holotype).

Sticta fossulata f. *expallida* Krempelh. in *Verh. zool.-bot. Ges. Wien* **30**: 336 (1881). – *S. cellulifera* f. *expallida* (Krempelh.) Stizenb. in *Flora, Jena* **81**: 114 (1895). Type: New Zealand, Napier, *C. Sturm*, ex Herb. Mus. Melb. (M! – holotype).

Sticta fossulata var. *subcyphellata* Nyl., *Lich. N.Z.*: 37 (1888*b*). – *S. flotowiana* var. *subcyphellata* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **3**: 346 (1925). Type: Nova Zelandia, prope Dunedin, Oct. 1861, *Dr Lauder Lindsay* (H-NYL 33478! – holotype).

Pseudocyphellaria billardierei sensu D. Galloway & P. James, non Delise, in *Lichenologist* **12**: 293 (1980).

Note 1: *Sticta richardi* var. *rufovirescens* Church. Bab.
Babington (1855: 278) writes of this taxon 'This form is in general easily distinguished from the following [*P. faveolata*] by certain relative characters, such as a softer, more opaque, and paler thallus, more naked and paler under side, also by the *strictly marginal* apothecia, whose disc we have never seen pruinose, and by the invariably (?) snowy cyphellæ; but when the plant assumes the form well represented by M. Richard (our var. β), it becomes less easy to separate it from *S. foveolata γ*, and we have seen a Tasmanian specimen or two so ambiguous that we fear the plants may possibly pass into each other, as Dr. Hooker has also strongly suspected'.

Galloway & James (1980: 293) referred *P. rufovirescens* to *P. billardierei*, a misinterpretation of this species widely held since the 19th century. However, the rediscovery of authentic material of *Sticta billardierei* (see Renner & Galloway, 1982; Galloway *et al.*, 1983*b*; Galloway & James, 1986) led to the raising of Babington's varietal name to specific rank for this distinctive, endemic species. A fine coloured engraving [as *Sticta carpoloma* sensu A. Richard] of *P. rufovirescens* is given in Richard (1833), and his description of the species (Richard, 1832) indicates white and not the yellow pseudocyphellae which are characteristic of *Sticta carpoloma* Delise. Montagne (1835, 1845) recognized Richard's description of *S. carpoloma* as referring to another species, one different from *S. carpoloma* Delise, and he accordingly described *S. richardi* for it, basing the name on material from Juan Fernandez collected by Bertero. In his 1845 paper Montagne refers all similar New Zealand material (including the type of *P. rufovirescens*) to *S. richardi.* However, the Juan Fernandez material is distinctive chemically and morphologically from *P. rufovirescens* in New Zealand, and consequently the several 19th century references to *S. richardi* in New Zealand refer to *P. rufovirescens.*

A specimen from Delise's herbarium (1836), collected in New Zealand, is labelled by him '*Sticta billardieri* var. β' and is referable to *P. rufovirescens* (G9002914!).

Morphology: Thallus irregularly spreading, often in large, entangled clones, 7–15(–50) cm diam., loosely attached, apices free, ascending, corticolous. *Lobes* linear-elongate, 5–8(–25) mm wide, 5–10(–15) cm long, ± dichotomously branching, contiguous or discrete, rarely imbricate, apices divergent, rounded, truncate or shallowly furcate. *Margins* entire, ridged above, ridge to 1 mm wide, rounded, also ridged below and there with occasional punctiform, white pseudocyphellae. *Upper surface* bright lettuce-green suffused brown or red-brown in parts when moist, pale grey-green, pale olivaceous to fawnish or red-brown when dry, conspicuously faveolate, interconnecting ridges broad, rounded 0·5–2 mm wide, faveolae shallow, matt, smooth, without isidia, soredia, maculae, phyllidia or pseudocyphellae. *Cephalodia* immersed, to 2 mm diam., visible as hemispherical swellings on both upper and lower surfaces. *Medulla* white. *Photobiont* green. *Lower surface* white to pale whitish pink or buff at margins, slightly darker centrally, shallowly bullate with a conspicuous, ± continuous marginal ridge and short, irregular ridges or puckers, or wrinkled below interconnecting ridges of upper surface, mainly glabrous, rarely patchily white-tomentose in older parts, *Pseudocyphellae* white, fleck-like, minute at margins, 0·1–1 mm diam. centrally, flat to shallowly excavate and with a slightly raised margin concolorous with lower surface. *Pycnidia* common at margins and on interconnecting ridges of upper surface, in clusters or rows, minute, black or red-brown, 0·1 mm diam. or less,

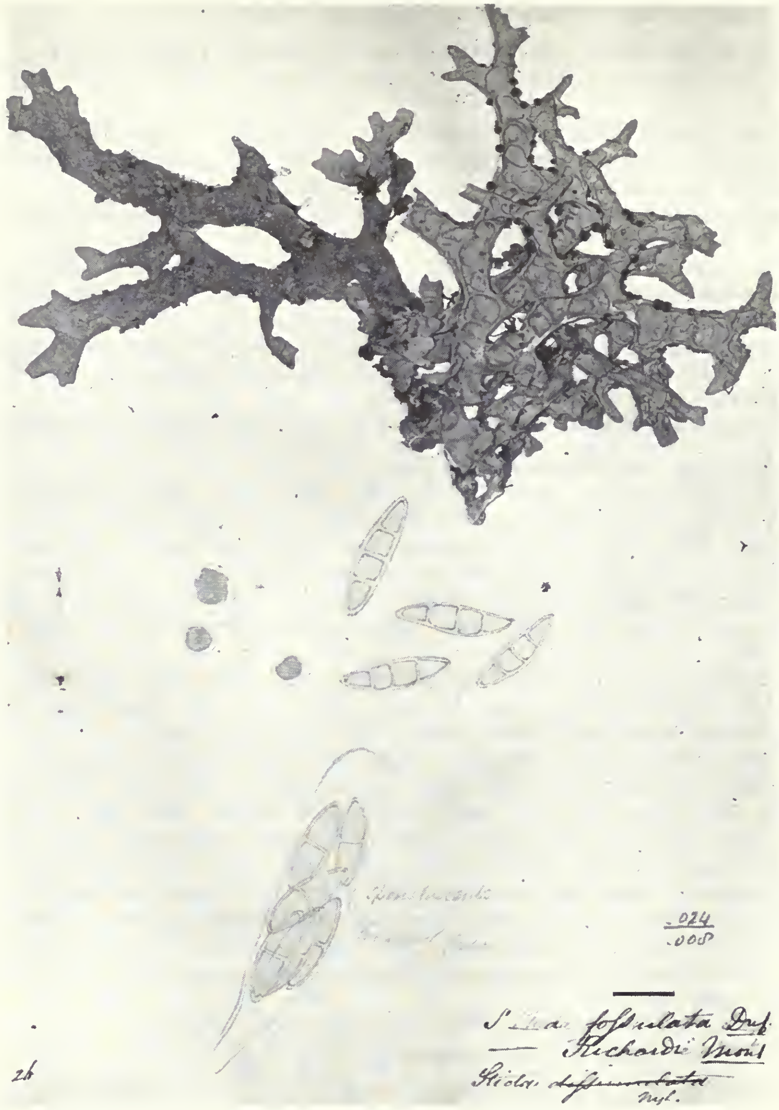

Fig. 119 *Pseudocyphellaria rufovirescens. Knight*, sine loco (WELT). Scale = 1 cm.

slightly rounded to punctate-impressed, eroding and leaving small pits. *Apothecia* marginal, concave at first, plane or convex at maturity, occasional to numerous, sessile, 1–3(–5) mm diam., disc pale brown-pink to red-brown matt or shining, epruinose, margins persistent, pale flesh-coloured, delicately crenate, exciple pale whitish buff, translucent when moist.

Anatomy: *Thallus* (250)300–800 µm thick. *Upper cortex* 64–102 µm thick, upper 11-15 µm pale orange-brown, cells compressed, remainder colourless, cells 4–11·5 µm diam. *Photobiont layer* 45–73 µm thick, *photobiont* green, cells rounded, 11–14 µm diam. *Medulla* 135–230(–550) µm thick, colourless, hyphae 3–4·5 µm diam. *Lower cortex* 30–70(–90) µm thick, outermost layer (11 µm) orange-brown, translucent, remainder pale straw-yellow, cells 4·5–9 µm diam. *Tomental hairs* occasional, 45–65(–120) µm long. *Apothecia: Exciple* colourless, 110–185 µm thick, cells 6·5–14 µm diam. *Hypothecium* 90–140 µm thick, dilute yellow-brown. *Thecium* colourless, 130–165 µm tall; *epithecium* poorly developed 11–15 µm thick, very pale yellow-brown, paler in

K. *Asci* 120–132 × 15–18 μm. *Ascospores* pale yellow-brown, fusiform to oval-ellipsoid, 3-septate at maturity (23–)27–36 × 7–9 μm.

Chemistry: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

Distinguishing features: *Pseudocyphellaria rufovirescens* is a large, endemic species with linear-elongate, dichotomously branching lobes, with truncate or shallowly furcate, divergent apices, and entire, ridged margins. The upper surface is shallowly faveolate, the interconnecting ridges broad and rounded and developed fully across the lobes. It has a white medulla, a green photobiont, and a pale or white, bullate, lower surface which is generally pale and glabrous or occasionally sparsely tomentose, with scattered, minute, white, fleck-like pseudocyphellae. Apothecia marginal, sessile, often numerous, disc pale red-brown or pinkish brown, exciple pale. Epithecium pale yellow-brown, unchanged in K. Spores pale yellowish brown, 3-septate. Chemistry of two hopanes [Code A of Wilkins & James (1979)].

Variation: *Pseudocyphellaria rufovirescens*, which often reaches a very great size in tangled clones to 50 cm diam., is a remarkably uniform species, showing only a slight variation in the amount of tomentum present on the lower surface. Generally, tomentum is not developed to any great extent, even in mature plants, and when present is confined to a few thin patches centrally; the apical lobes are always glabrous. It is distinguished from both *P. billardierei* and *P. faveolata* by the pale red-brown apothecia, the pale spores, the pale epithecium (unchanged in K), the pale, ± glabrous lower surface, the flat, fleck-like pseudocyphellae, and a different chemistry (*P. rufovirescens* is Code A, while *P. billardierei* is Code C and *P. faveolata* Code B). *P. carpoloma* superficially resembles exposed forms of *P. rufovirescens*, but has a dark red-brown lower surface which is ± tomentose, prominent yellow pseudocyphellae (especially along lobe margins), brown-black to black apothecia, brown spores, and a different chemistry [Code D of Wilkins & James (1979)]. See also Table 2. The widespread tropical species *P. sulphurea* is somewhat similar to *P. rufovirescens* in terms of lobe morphology and also has a pale, glabrous lower surface and an identical chemistry, but its upper surface is quite distinctive being smooth, punctate-impressed and not at all reticulate-faveolate. *P. rufovirescens* is distinguished from *P. murrayi* (the two species form photosymbiodemes in some localities) which has smoother, undulate, seldom faveolate lobes which are expanded at the apices, a blue-green photobiont, a ± consistently uniform tomentum on the lower surface, and dark brown to black apothecial discs.

Distribution: (Fig. 120) Widespread throughout New Zealand from North Auckland (lat. 35°S) southwards to Stewart I., and the Auckland Is, lowland to subalpine, sea-level to 1200 m.

Habitat ecology: *Pseudocyphellaria rufovirescens* is a familiar and widespread lichen in New Zealand. Mainly a lowland species, it reaches a great size in cool, humid, moist habitats in partial shade. It is a common epiphyte of tree trunks, the twigs and branches of small trees and shrubs, and will cover rotting logs in damp, shaded habitats, although it is absent from densely shaded sites where species such as *P. dissimilis*, *P. cinnamomea*, and *P. fimbriatoides* can thrive. In full sunlight specimens of *P. rufovirescens* are often suffused red-brown. In damp gullies, and on shrubs along stream beds, especially in central North I., *P. rufovirescens* forms photosymbiodemes with *P. murrayi*.

It is known from mixed podocarp-hardwood forest or forest remnants, from beech-podocarp forest, and from scrubby areas where *Leptospermum* is an important successional element. It is an epiphyte of the following phorophytes: *Agathis australis*, *Alsophila smithii*, *Beilschmiedia taraire*, *B. tawa*, *Carpodetus serratus*, *Coprosma spp.*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Fuchsia excorticata*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Metrosideros lucida*, *Laurelia novae-zelandiae*, *Myrtus bullata*, *Nothofagus fusca*, *N. menziesii*, *Podocarpus hallii*, *P. totara*, *Pennatia corymbosa*, *Pseudopanax crassifolius*, *Pseudowintera colorata*, *Rubus australis*, *Senecio eleagnifolius*, and *Weinmannia racemosa*.

Lichens commonly associating with *P. rufovirescens* include *Dendriscocaulon dendriothamnodes*, *Everniastrum sorocheilum*, *Hypotrachyna sinuosa*, *Leioderma amphibolum*, *L. pyc-*

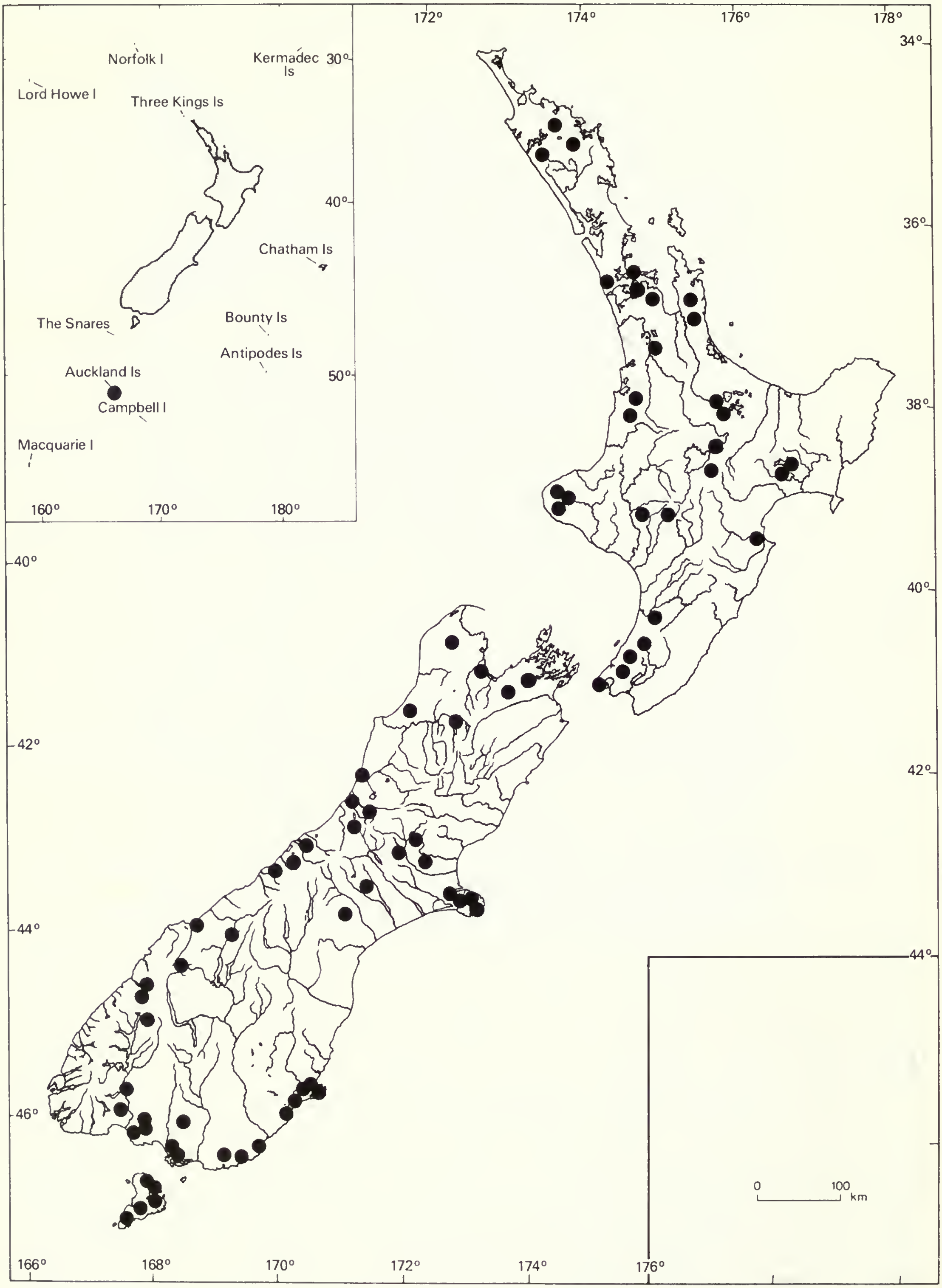
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Fig. 120 Distribution of *Pseudocyphellaria rufovirescens.*

nophorum, *Leptogium azureum*, *Lobaria adscripta*, *L. scrobiculata*, *Physma chilense*, *Pseudocyphellaria billardierei*, *P. dissimilis*, *P. faveolata*, *P. glabra*, *P. homoeophylla*, *P. hookeri*, *P. intricata*, *P. multifida*, *Sphaerophorus notatus*, *S. tener*, *Sticta caliginosa*, *S. filix*, *S. lacera*, *S. latifrons*, *S. subcaperata*, and *Usnea torquescens*.

Specimens examined: 264.

47. **Pseudocyphellaria sericeofulva** D. Galloway **Fig. 121**

in *Lichenologist* **15**: 144 (1983). Type; New Zealand, North I., South Auckland, Kopuku coalmine near Mercer, on *Cordyline australis*, 1 May 1981. *J. K. Bartlett* (CHR 375961! – holotype, BM! – isotype).

Description: *Thallus* (3–)5–10(–15) cm diam., of closely imbricate lobes, rather loosely attached, corticolous. *Lobes* rounded to ± irregularly cochleate, crowded, densely imbricate, ± subascending at margins, short, 0·2–0·6(–1) mm diam. *Margins* noticeably thickened below, ± subascendent, shallowly notched, crenate to ± pectinate, conspicuously pseudocyphellate, pseudocyphellae punctate to short-linear, often ± swollen. *Upper surface* dark slate-blue to glaucous blue-grey, sometimes suffused red-brown when wet, pale greyish or blue centrally, suffused red-brown towards apices when dry, very shallowly bullate in parts, mainly smooth,

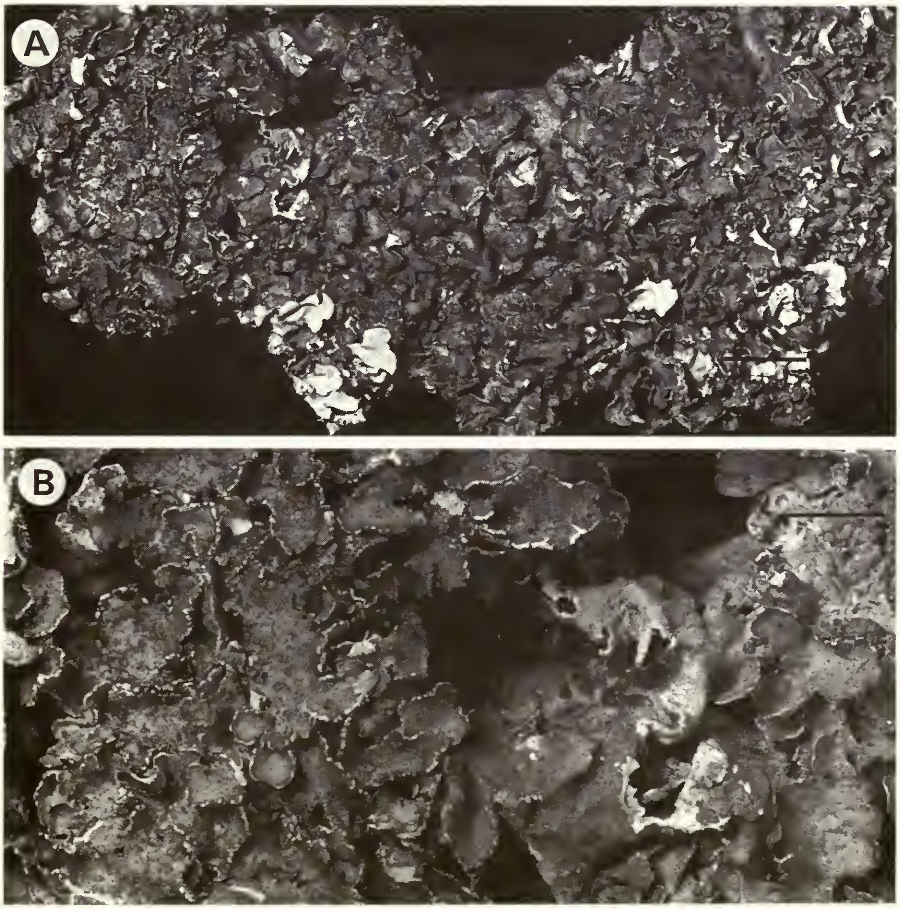

Fig. 121 *Pseudocyphellaria sericeofulva*. Isotype (BM). A. Scale = 1 cm. B. Scale = 4 mm.

somewhat convex-undulate, especially near margins, matt, often ± glabrous at margins, lightly to moderately densely white-tomentose centrally, tomentum rather scattered, silky, rarely densely developed, maculae common and distinctive both at margins and towards centre, in a yellow, reticulate pattern, best seen when wet (× 10 lens), giving a mottled or marbled appearance to lobes, isidia and soredia absent, pseudocyphellae occasional, randomly scattered, yellow, solitary, never confluent, punctate to ± raised, often projecting from tomentum and closely resembling those of lower surface. *Medulla* white. *Photobiont* blue-green. *Lower surface* pale creamish yellow at margins, darkening and becoming dark brown or ± blackened centrally, conspicuously wrinkled, puckered or ridged or in part ± bullate, in places ± glabrous to delicately and continuously pilose, tomentum fine, velvety, whitish, very short, thicker and ± brown to black in parts. *Pseudocyphellae* yellow, conspicuous, scattered, noticeably raised, on ± conical verrucae, most often on ridges and wrinkles, decorticate area convex to plane, rarely excavate, 0·01–0·1 mm diam., ± rounded. *Apothecia* not seen.

Anatomy: *Thallus* 180–250(–320) μm thick. *Upper cortex* 20–30(–45) μm thick, of 7–9 rows of colourless to pale straw, thick-walled, round to irregular, ± isodiametric cells, walls angularly thickened, upper 12 μm or cells compressed, stretched, remaining 20 μm of cells (4–6 rows) broader, walls to 2 μm thick, lumina round to irregular 2–4·5 μm diam., *Tomental hairs* arising from upper surface, 4–5 μm thick, colourless, thick-walled, septate, solitary or in fascicles, 20–55 μm long. *Photobiont layer* 70–100 μm thick, yellowish olive in upper 20–27 μm, remainder of zone blue-green, hyphae interwoven between packets of *Nostoc*, enclosed in a gelatinous sheath. *Medulla* 90–110(–165) μm thick, very lax, loosely arranged, colourless hyphae to 4·5 μm diam., encrusted in parts with small yellow crystals. *Lower cortex* 15–20 μm thick, of 2–3 rows of pale, straw-coloured to dilute brownish, thick-walled, ± isodiametric cells, walls 2–2·5 μm thick, lumina round to irregular to 4·5 μm diam. *Tomental hairs* in bundles, ± concolorous with lower cortical cells, 4–5 μm diam., septate, thin-walled, 45–90(–150) μm long.

Chemistry: tenuiorin, methyl gyrophorate, hopane-7β, 22-diol (tr.), hopane-6α, 7β, 22-triol, 7β-acetoxyhopane-6α, 22-diol (tr.), 6α-acetoxyhopane-7β, 22-diol (tr.), unidentified triterpenoid, norstictic (tr.), stictic, cryptostictic (tr.), and constictic acids, an unidentified depsidone, and pulvinic acid, pulvinic dilactone, and calycin.

Distinguishing features: *Pseudocyphellaria sericeofulva* is a rather rarely collected, endemic species having short, rounded, imbricate-crowded, somewhat cochleate lobes, with crenate to pectinate margins which are noticeably pseudocyphellate. The upper surface is smooth or shallowly bullate, distinctly maculate (× 10 lens) and with scattered, moderate to dense, pale fawn or whitish, laminal tomentum, without soredia, isidia, or phyllidia. It has a white medulla, a blue-green photobiont, and a pale buff, tomentose lower surface with conspicuous, scattered, yellow pseudocyphellae. It is not known fertile. The chemistry is complex, identical with that of *P. crocata* to which it is closely related. It has a distinctive, fishy smell (? methylamine) when moistened.

Variation: *Pseudocyphellaria sericeofulva* is still poorly collected being known from only four gatherings and hence it is still premature to speculate on the morphological variation in the species. Those specimens seen all have a uniform morphology. *P. sericeofulva* is closely related to *P. crocata*, having the same chemistry but with somewhat cochleate-imbricate lobes which are not faveolate-ridged or sorediate either at the lobe margins or laminally, but which here and there are tomentose.

Distribution: (Fig. 122) North I., from Radar Bush to Mercer (South Auckland), mainly lowland and coastal, 100–200 m. On *Cordyline australis*, *Podocarpus totara*, *Rhabdothamnus solandri*, and *Sophora*.

Specimens examined: North Island. North Auckland: Radar Bush, January 1980, *J. K. Bartlett* 18895 (BM, Herb. Bartlett); Pipiwai 40 Km NW of Whangarei, July 1984, *J. K. Bartlett* 28895, 28897, 28898 (BM, Herb. Bartlett); South Auckland: Kopuku Coal mine near Mercer, May 1981, *J. K. Bartlett* (BM, CHR 375961, Herb. Bartlett).

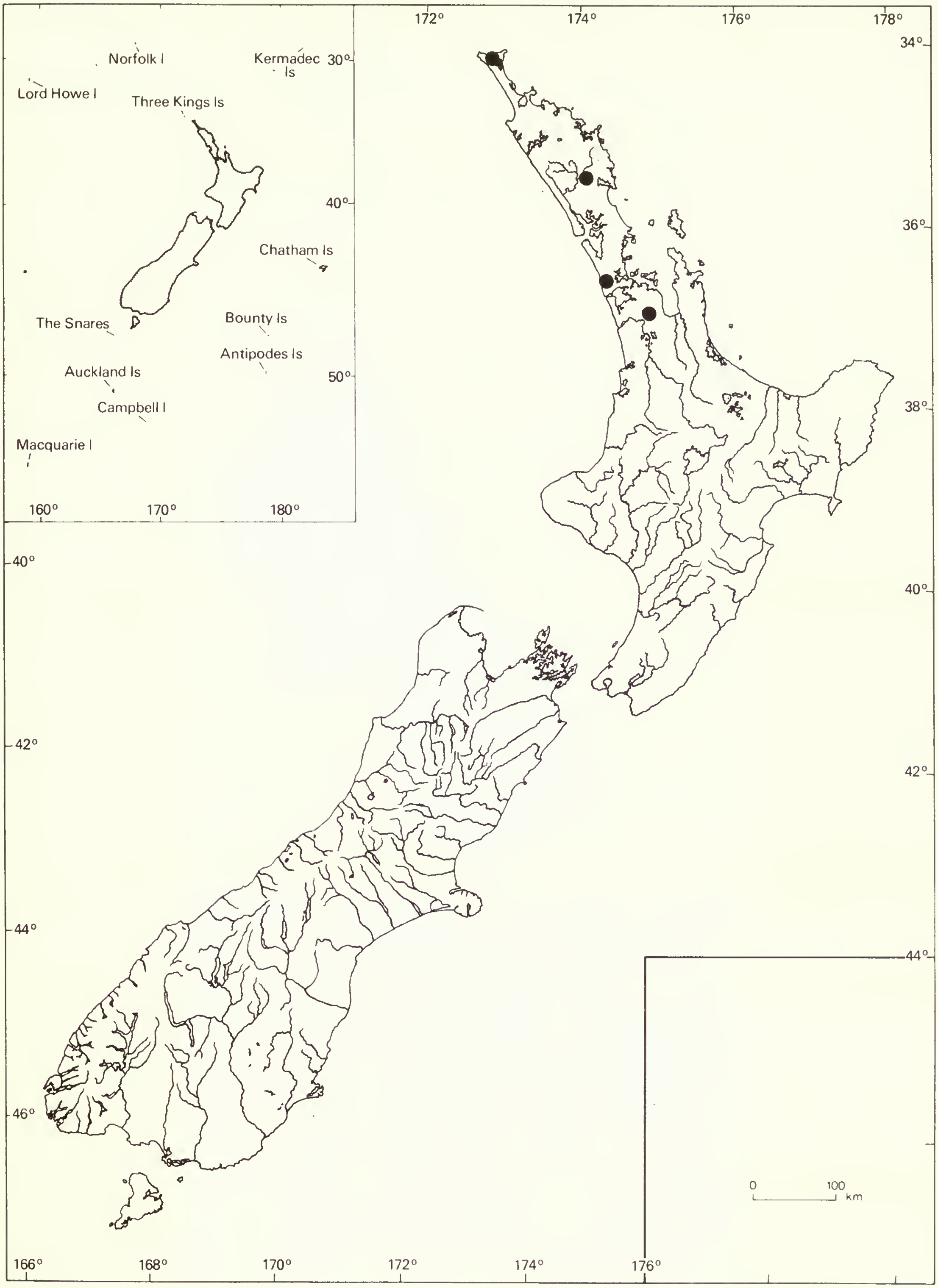
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Fig. 122 Distribution of *Pseudocyphellaria sericeofulva*.

48. Pseudocyphellaria wilkinsii D. Galloway, sp. nov. Fig. 123

Diagnosis: Pseudocyphellariae epistictae similis, sed thallus fragilis, margo isidiatus, vel phyllidiatus, supra pseudocyphellatus, pseudocyphelliis dispersis, ad marginem isidiatis. Paraphysibus submoniliformibus, epithecio dilute isabellino, K non mutato, sporae ellipsoideae, 1-3-septatae, 27–34 × 7–9 μm. Typus: New Zealand, sine loco, *C. Knight* ex Herb. Leighton (BM! – holotype). [t.l.c.: 7β-acetoxyhopan-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol].

Morphology: Thallus orbicular to spreading, 3–12(–20) cm diam., closely attached from centre to margins, or with margins ± free, corticolous. *Lobes* short and rounded to ± linear-elongate, 5–8(–12) mm wide, 5–15(–25) mm long, ragged, deeply incised, complex-imbricate at margins and centrally or with larger apical lobes, ± discrete. *Margins* rarely ±

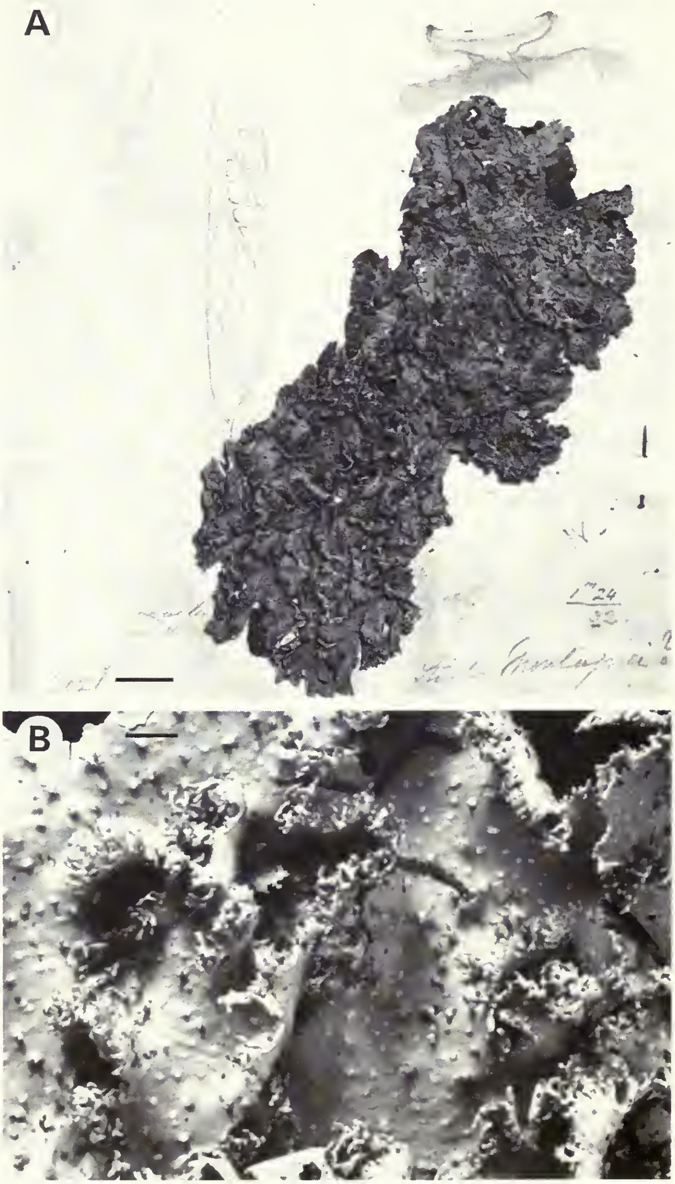

Fig. 123 *Pseudocyphellaria wilkinsii*. A. Holotype (BM). Scale = 1 cm. B. Cape Karikari, Matai Bay, *Tibell* 14903 (UPS). Scale = 1 mm.

rounded, to ragged-incised or crenate, ± sinuous and slightly ascending, moderately to densely isidiate-phyllidiate. *Upper surface* undulate or plane, occasionally shallowly wrinkled or ridged, occasionally dimpled-papillate (cephalodia), glaucous green when moist, pale grey-green or fawnish often suffused red-brown when dry, matt or shining, without soredia or maculae, phyllidiate-isidiate and pseudocyphellate. *Phyllidia* primarily marginal but also spreading onto lamina, often in a dense crust and in central parts thallus may be totally obscured by dense crust of phyllidia, flattened, to 0·1 mm wide and to 1 mm tall, subdichotomously to complexly branching, subterete in parts, apices often inflated. *Isidia* marginal and laminal, at first minute, terete, to 0·1 mm tall and 0·02–0·05 mm wide, then expanded-glomerulate and branching, becoming loosely to densely coralloid, fragile, easily broken from lamina and leaving pits, also associated with margins of pseudocyphellae, more common in older parts of thallus, at length becoming flattened-phyllidiate. *Pseudocyphellae* sparse to frequent, scattered, minute, punctiform near margins, to 0·2 mm diam., rounded to occasionally ± linear centrally, often surrounded by groups of minute, globular, fragile isidia. *Medulla* white. *Photobiont* green. *Lower surface* whitish to pale fawn or yellowish, slightly darker centrally, often glabrous, shining, wrinkled in a narrow, marginal zone, elsewhere evenly and thickly tomentose, tomentum pale fawn to dark red-brown, close and ± velvety, to shaggy-arachnoid. *Pseudocyphellae* very rare, best seen at or near margins, white, flat, fleck-like, to 0·1 mm diam. *Apothecia* rare, scattered, solitary, laminal or submarginal, sessile, constricted at base, 0·5–2·5 mm diam., rounded to subirregular, shallowly concave to plane or ± undulate, disc pale red-brown to medium red-brown, margins persistent, minutely crenate-scabrid, pale flesh-coloured, matt, epruinose, exciple pale buff or whitish to very pale red-brown, minutely verrucose-areolate, ± translucent when moist, not phyllidiate or isidiate, massive and obscuring disc when young.

Anatomy: *Thallus* 100–140 μm thick. *Upper cortex* 27–34 μm thick, outer parts pale yellowish, cells compressed, remainder colourless, cells 2·5–7 μm diam. *Photobiont layer* 11–16 μm thick, almost centrally placed, *photobiont* green, cells round to irregular, 4·5–7 μm diam. *Medulla* dense, colourless, 45–70 μm thick. *Lower cortex* 18–22 μm thick, colourless or pale straw-yellow in outermost parts, cells 2·5–6 μm diam. *Apothecia : Exciple* 90–140 μm thick, colourless, outer surface in ragged, pyramidal clumps (scabrosity). *Hypothecium* 45–55 μm thick, pale yellowish to fawn, unchanged in K. *Thecium* 70–80 μm tall, colourless; *epithecium* 11–15 μm thick, translucent, pale yellow-brown, unchanged in K; *paraphyses* submoniliform at apices. *Asci* 70–82 × 15–18 μm. *Ascospores* brown, 1-3-septate, ellipsoid, apices rounded or pointed, contents vacuolate, 27–34 × 7–9 μm.

Chemistry: As above.

Pseudocyphellaria wilkinsii is named for Dr A. L. Wilkins, Chemistry Department, Waikato University, Hamilton, New Zealand, for his researches into the triterpenoid chemistry of *Pseudocyphellaria*.

Distinguishing features: *Pseudocyphellaria wilkinsii* is an apparently endemic species having short and rounded, to somewhat linear-elongate, rather ragged, fragile lobes with incised, isidiate-phyllidiate margins. The upper surface is pseudocyphellate, the pseudocyphellae occasionally being associated with fragile, terete, simple to coralloid isidia (Fig. 123B). It has a white medulla, a green photobiont, and a pale lower surface, tomentose centrally with glabrous margins. Apothecia are rare, the exciple lacks isidia or phyllidia, the epithecium is pale yellow-brown (unchanged in K), and spores are brown, 1-3-septate. It has a two-hopane chemistry [Code A of Wilkins & James (1979)].

Variation: *Pseudocyphellaria wilkinsii* shows some variation in thallus size and morphology of lobes, depending on local ecological conditions, though in general it is a rather uniform species. Sterile forms are most often collected. It is closely related to *P. episticta* and in several earlier accounts (Ronaldson & Wilkins, 1978; Galloway & James, 1980; Galloway *et al.*, 1983*b*; Galloway, 1985*b*) the description of *P. episticta* includes *P. wilkinsii* which was treated as a

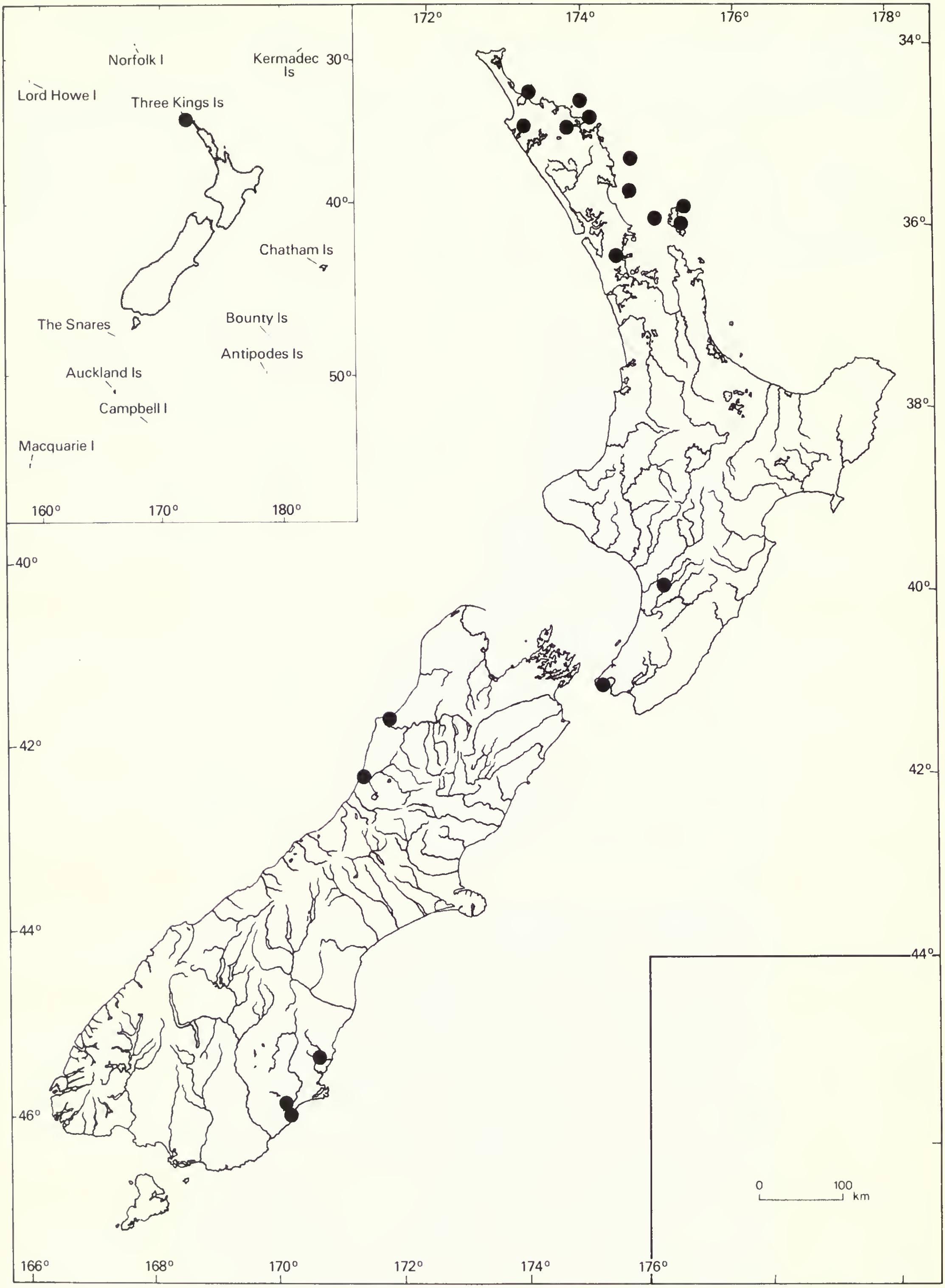
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Fig. 124 Distribution of *Pseudocyphellaria wilkinsii.*

chemodeme of *P. episticta*. *Pseudocyphellaria wilkinsii* differs from *P. episticta* in chemistry, in the negative epithecium reaction in K, in the marginal and laminal isidia, and in the generally thinner and more fragile nature of the lobes.

Pseudocyphellaria wilkinsii is distinguished from *P. chloroleuca* by the tomentose lower surface, the pseudocyphellate upper surface, the broader and ± plane to convex lobes which are not at all canaliculate, and by the chemistry [*P. wilkinsii* is C−]. The presence of isidia, phyllidia, and laminal pseudocyphellae distinguish *P. wilkinsii* from *P. multifida*. Some sun-exposed forms of *P. wilkinsii* are suffused red-brown or brown-black and resemble forms of *P. argyracea*; however, this latter species has a blue-green photobiont.

Distribution: (Fig. 124) Three Kings Is, (lat. 34°S) to Manawatu (Wellington) in North I., and spasmodically in South I., in Nelson (near Westport), Westland (Greymouth) and Otago (Maungatua, Mt Watkin, Taieri Mouth); mainly northern and coastal, lowland, sea-level to 510 m.

Habitat ecology: *Pseudocyphellaria wilkinsii* is most commonly collected from trees and shrubs, or from soil below these in northern coastal forest between lats 35°6′S and 37°S. It is recorded from many northern offshore islands as *P. episticta* and appears to prefer habitats of moderate to low rainfall and with high summer temperatures. It is known from the following phorophytes: *Avicennia marina* var. *resinifera*, *Cordyline australis*, *Dacrycarpus dacrydioides*, *Kunzea ericoides*, *Leptospermum scoparium*, *Metrosideros excelsa*, *Nothofagus menziesii*, *Prumnopitys taxifolia*, and *Rhopalostylis sapida*. In northern habitats it associates with the following lichens: *Lobaria asperula*, *Leptogium azureum*, *Nephroma rufum*, *Normandina pulchella*, *Parmotrema reticulatum*, *P. tinctorum*, *Pseudocyphellaria aurata*, *P. chloroleuca*, *P. montagnei*, *P. poculifera*, *Sticta latifrons*, and *S. squamata*.

Specimens examined: 35.

Acknowledgements

I am most grateful to the curators of the herbaria mentioned in the text for the provision of type and other material, and particularly to Mme Locquin (Paris), Patricia Geissler (Geneva), Orvo Vitikainen (Helsinki), Brian Coppins (Edinburgh), Roland Moberg (Uppsala), Hannes Hertel (Munich), Patrick Brownsey (Wellington), and Bryony Macmillan (Lincoln). Many people have allowed me access to their personal collections, and I thank them most sincerely for offering me the opportunity to study these, especially Rolf Du Rietz, Greta Du Rietz*, and Hugo Sjørs (Uppsala) for arranging access to the collections of G. Einar Du Rietz*; Lief Tibell (Uppsala), Helmut Mayrhofer (Graz), Volkmar Wirth (Stuttgart), Jack Elix (Canberra), Henry Imshaug (East Lansing), Harrie Sipman (Berlin), Gunnar Degelius (Askim), and Bruce & Glenys Hayward (Lower Hutt). A special debt of gratitude is due to my late friend John Bartlett* who, over some eight years, assiduously collected extensive suites of specimens from all parts of New Zealand, without which this study would have been very much the poorer. It has been a pleasure to me to record his association with this work in the name *Pseudocyphellaria bartlettii*.

I was very greatly assisted over some 20 years in New Zealand field studies by the following friends and colleagues: Nancy Adams, Suzanne & Heinz* Aufricht, John Bartlett*, Betty Batham*, John Braggins, Geoff Bratt*, Geoff Baylis, Margaret Bulfin, Euan Cameron, Nancy Cawley, John Child*, Peter Child*, Beverley & Bruce Clarkson, Ted Corbett, Mavis Davidson, Austen Deans, Chris Eckroyd, Denis Fogg, Alan Green, Eric Godley, Bruce & Glenys Hayward, John Holloway, Peter Johnson, Lawrence Kennedy, Tom Kennedy, Willy Kuschel, Sam & Joy McClimont, Alan Mark, Colin Meurk, Brian Molloy, Peter Smith, Philip Temple, Alistair Wilkins, Hugh Wilson, and Lloyd Wilson*.

For helpful discussion on taxonomic and nomenclatural matters, and for the provision of scarce literature and/or exsiccata material I am grateful to Ove Almborn (Lund), Lars Arvidsson (Göteborg), Hannes Hertel (Munich), Henry Imshaug (East Lansing), Jack Laundon (London), and Rolf Santesson (Stockholm & Uppsala).

Colleagues at the British Museum (Natural History) were unfailingly helpful at all stages of the work and

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* deceased.

I thank especially Joy White for all her work in arranging loans and curating herbarium material; Derek Adams, Phil Crabbe, Phil Hurst, Jackie Lovell and Paul Lund (BM photographic Unit) for their expert photographic assistance; and Sue Barnes and Don Claugher for their help with SEM studies. Travel funds from the Museum for fieldwork in New Zealand in 1983, and herbarium work in Boston and East Lansing in 1986 (Park Fund), are gratefully acknowledged. Finally, I would like to record my grateful thanks to Peter James (BM) who originally suggested this study, and whose constant advice, encouragement and help have been mainstays of my work. He made exhaustive comments on several drafts of text and also assisted with chemistry and in the preparation of the illustrations.

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MACROLICHENS OF EAST AFRICA

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Summer 1988, 384pp (approx.), 185 figs., 16pp colour illustrations.
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Photoset by Rowland Phototypesetting Ltd, Bury St Edmunds, Suffolk
Printed in Great Britain by Henry Ling Ltd, Dorchester